Ecological Studies of *Hieracium pilosella* and *H. praealtum*

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Frontispiece. *Hieracium pilosella* and

H. praealtum

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ABSTRACT

The ecology of *Hieracium pilosella* and *H. prealtum* in short tussock (*Festuca novae-zelandiae*) grasslands was investigated using a multifactorial approach. *H. pilosella* is an invasive species of grazed, moderate to sparsely vegetated habitats, while *H. praealtum* is an opportunist coloniser of vegetation gaps. Although *H. prealtum* co-existed with other pasture species, *H. pilosella* expanded into adjoining vegetation and eliminated most species. *H. pilosella* has considerable interference potential (competition and allelopathy) and regenerative advantages (vegetative reproduction) over *H. praealtum* and other resident species. Although the ecological behaviour, seasonal growth pattern, and dry matter production of *H. pilosella* are deleterious to short tussock grasslands, the presence of *H. praealtum* is of some agronomic value in them.

CHAPTER 1

INTRODUCTION

1.1 GENERAL INFORMATION

Background

Several species of the genus *Hieracium* (Compositae), commonly termed hawkweeds, were naturalised in New Zealand at least fifty years ago (Allan 1940, Healy 1976). For many years members of this genus were relatively unimportant as an element of the flora and agronomically. During the last twenty-five years or so, several species have appreciably expanded their populations. *H. praealtum* and particularly *H. pilosella* have become some of the main species in the modified short tussock grasslands of the lower run country in the South Island where they are considered to be serious weeds (Anon. 1976, Healy 1976, Makepeace 1976). Further increases in distribution and abundance seem likely. *H. pilosella* is notable for the formation of extensive almost pure populations (frontispiece and plate 1.1) which appear to reduce agricultural productivity. *H. pilosella* presents a weed problem in other agricultural regions of the world (Becker and Guyot 1951, Bingham 1965, Hay and Ouelette 1959, Voss and Böhlke 1978). However, there is little knowledge of its ecological behaviour, biology and dry matter production especially in New Zealand (Anon. 1976). No information is available on control except with herbicides (Matthews 1975). Even when biologically effective, these chemicals may not be

Plate 1.1 *Hieracium pilosella* in fescue-tussock (*Festuca novae-zelandiae*) grassland on Wolds Station.

economically viable given the low capital return per unit area of land in the affected areas of the high country.

Research rationale

The aim of this study was to examine the biology of *H. pilosella* in the context of the short tussock (*Festuca novae-zelandiae*) grasslands and to provide ecological and agronomic perspectives on this hawkweed. The research approaches used in plant ecology studies have been divided by Grime (1965) into comparative, direct, and correlative types. The comparative approach involving the study, under standardised experimental conditions, of life-history stages and events of two or more species was the method used throughout this work. *H. praealtum* was used as the contrast species because of both its apparent ecological differences and importance as the second most common and widespread hawkweed. *H. lachenalii* was used in one experiment for comparison. Although this species is reported to be increasing in some areas (Dunbar 1977) it is rare in the Mackenzie Basin.

On the basis of a literature search (reviewed in the appropriate chapters) and preliminary field work, certain aspects of the life history of *H. pilosella* which were considered important to the success of this species were selected for intensive study namely: phenotypic and chromosomal (ploidy) variation; reproductive biology; growth and production; germination behaviour; morphological responses to light gradients and shading; soil fertility responses and modifications; interference phenomena, particularly allelopathy; phytosociology; management

influences and chemical control.

Taxonomy and distribution of the study species

Except for *H. pilosella*, there is uncertainty as to the exact identity of the species in New Zealand. The the treatment given by Healy (1976) is followed here but caution should be exercised in comparing New Zealand plants with Northern Hemisphere plants with the same species name. The taxonomic problems in *Hieracium* are due to a high incidence of apomixis, polyploid series and polymorphism (Sell and West 1976). For this reason, much of the earlier taxonomy produced many false species (Turesson and Turesson 1960) which have only recently been deleted (Sell and West 1976). A major revision using chemotaxonomic procedures (Bate-Smith *et al.* 1968, Sell and West 1976) seems imminent.

According to Healy (1976) and Sell and West (1976), two of the three hawkweed species, *H. pilosella* and *H. praealtum*, used in this study belong to the subgenus *Pilosella* while the third species, *H. lachenalii*, belongs to the subgenus *Hieracium*. The subgenus *Pilosella* contains sexual or partially (facultative) apomictic species, the majority of which also reproduce vegetatively by stolons. Intermediates, some of which are of certain hybrid origin, occur between nearly all known forms in Europe. The subgenus *Hieracium* contains several thousand microspecies which are all non-stoloniferous and usually apomictic (agamospermic).

The distribution of the two main species and *H.*

lachenalii used in this study were (Anon. 1976, Healy 1976):

H. pilosella: the most widespread species, occurs from sea level to about 1 700 m altitude throughout most of the South and North Island; rare to locally abundant in modified tussock grassland and grassland on dry river terraces and stony flats. The highest abundance is reached in the short tussock grasslands of montane Canterbury, Marlborough and Otago.

H. praealtum: rare to locally abundant on dry river terrace country and in modified tussock grassland in Marlborough, Canterbury and Otago. Recently reported from the North Island about Upper Atiamuri and near Taupo.

H. lachenalii: rare to locally abundant in modified low tussock grassland in Marlborough, Canterbury and Otago, growing in a range of habitats (e.g., grassland, riverbeds, slips, shaded banks). Reported in the North Island only from Mt. Egmont.

Ecological observations

Distinctive but highly overlapping distributions within tussock grassland habitats were evident for *H. pilosella* and *H. praealtum*. *H. pilosella* generally reached its greatest abundance on grazed, sunny aspects of low rainfall areas or physiologically dry habitats. *H. praealtum* was more abundant in slightly wetter areas or moister habitats such as on partially shaded southerly aspects, and particularly where grazing by sheep was infrequent or

absent. *H. praealtum* was a primary coloniser of exposed surfaces and its presence in closed grassland was usually dependent on previous soil exposure. In the absence of grazing on large exposed soil surfaces, *H. praealtum* frequently became dominant within two to three years. While *H. pilosella* successfully colonised a wider habitat range than *H. praealtum*, ranging from bare ground to closed low vegetation, it performed better in areas initially with low vegetation cover and only small amounts of bare ground. Establishment of both species from seed was poor on sites with frequent frost heave when grazed over winter. Vegetative reproduction was effective for both species over a broad range of habitat conditions.

The history of *H. pilosella* and *H. praealtum* in New Zealand

The means by which *H. pilosella* and *H. praealtum* were introduced to New Zealand are unknown. Impure seedlines imported for pasture development are suspected (Anon. 1976). Early records and herbarium specimens indicate the probable site of colonisation as being near Ashburton prior to 1919†. By 1920, *H. pilosella* was recorded as occurring in a few small patches near the Hinds River (Allan 1920) but later spread inland and was established in scattered parts of Canterbury and the Mackenzie Country (Allan 1940) used for extensive grazing. Although further increases in range continued (Barker 1953, Kerr 1950, Moore 1955, 1976),

† Earliest collection of *H. pilosella* was taken by H.H. Allen, Maronan Road, in 1919 and is held in the Herbarium, Botany Division, DSIR, Lincoln.

H. pilosella was still a rare species in many parts of the Mackenzie Country as late as 1963 (Connor 1964). At the beginning of this study in 1974, *H. pilosella* was a ubiquitous species in the Mackenzie Country. *H. pilosella* cover (area) of 5 to 20% was common and localised sites occurred with cover of more than 90%. A similar increase has been documented at Molesworth Station in Marlborough (Stevans and Hughes 1973, Moore 1976). In the late 1970's, several runholders in the upper Waitaki reported a decline of production related to *H. pilosella* increases.

H. praealtum has a similar history to *H. pilosella*. Recorded as well established near Peel Forest in 1920 (Allan 1920), *H. praealtum* spread to other inland areas of the South Island (Anon. 1976, Allan 1940, Stevans and Hughes 1973, Healy 1969). A large increase in abundance of *H. praealtum* occurred during the last 25 years (Anon. 1976) and it was recently recorded in two places in the North Island (Healy 1976).

The study areas

The main study area was in the Mackenzie Country (Fig. 3.1) of the South Island. This area was chosen because

(1) it was one of the regions most seriously affected by *H. pilosella*,

(2) sites were available at various stages of invasion by both *H. pilosella* and *H. praealtum*,

(3) soil and climate types representative of much of the South Island high country were represented within a

conveniently small geographic zone and

(4) logistic support in the Basin was available from Grasslands Division, DSIR.

The secondary study area was at Cave Stream near Castle Hill Station in mid-Canterbury, chosen for proximity to Christchurch.

The history, climate, geomorphology, soils, vegetation and fauna of the Mackenzie Country have been described by Connor (1964) and extensively reviewed by O'Connor (1976). The mid-Canterbury region is also described in Knox (1969). From these sources the Mackenzie Country is described as a plain at c. 500 m in the centre of the southern part of the South Island bounded on three sides by mountains. The Main Divide lies to the west and north. A series of ranges, the Two Thumb, Rollesby, Dalgety and Kirkliston run along the east with the Grampian mountains entering the plain from the Dalgety and Kirkliston Ranges. The basin is open to the south with the drainage systems of the Ohau and Waitaki Rivers.

The rocks of the region are a series of undifferentiated greywackes and argillites which are extensively covered in secondary deposits. The northern part of the basin is characterised by a series of extensive moraines and other landforms resulting from glacial and postglacial processes of the last Otiran glaciation. To the south extends a large outwash plain dissected with numerous streams and rivers indicating the recent fluvial phase.

The climate of the Mackenzie Basin is sub-continental, as a result of the intermountain position, unlike the temperate oceanic climate of much of New Zealand. The

summer period is hot as a result of intense solar radiation, although frosts may occur on clear nights. Winter is marked by consistently low temperatures produced by a combination of nocturnal cooling and cold air masses draining into the Basin. The rainfall is concentrated around the mountain perimeter and decreases rapidly towards the centre. Additional moisture is returned along the eastern ranges by the mist from cold air masses which regularly flow down the mountain slopes towards evening. Most parts of the Mackenzie Basin experience water deficits during at least part of the year. Dry weather, shallow well-drained soils with low moisture storage potential and strong Föhn winds from the north-western sector cause very high evapotranspiration deficits in the central region.

The soils are formed from greywacke, an arkosic sandstone with a high quartz and plagioclase feldspar content but deficient in weatherable basic minerals and consequently essential plant nutrients. The available nitrogen, phosphorus and sulphur status of the entire region is low as are some micro-nutrients, especially molybdenum. Sulphur deficiencies are greatest in the semi-arid zone to the southeast because of low atmospheric returns. Phosphorus and molybdenum deficiencies increase with higher rainfall particularly where retention of phosphorus is marked in the north-west sector.

The major part of the Mackenzie Country is grassland and formerly was mixed short and tall tussock grassland. Most of the former tall tussock (*Chionochloa rigida*) and red tussock (*C. rubra*) grassland on the plain was modified

to short or fescue tussock (*Festuca novae-zelandiae*) grassland by European man through burning and grazing practices. In the sub-arid central region the tussock has almost been eliminated in places and a complex flora has given way to a degenerate community often characterised by *Aira caryophyllea*, *Rumex acetosella* and *Vulpia bromides* with a semi-desert physiognomy. Rabbits were a severe problem until the last two decades when control measures reduced their population but they are still numerous. The effect of rabbit control has been the recovery of some of the depleted short tussock but also the release of several weeds (Harris 1968, Molloy 1964).

The general background of the Cave Stream site in mid-Canterbury is contained in the descriptions by Healy (1969). The Cave Stream site experiences greater rainfall than the lower parts of the Mackenzie Basin. Hawkweed communities were present on the shallower droughty soils.

Nomenclature and biometrics

Nomenclature used is that given by the New Zealand Weed and Pest Control Society (1969).

Univariate biometric procedure was based on Sokal and Rohlf (1969), Snedecor and Cockran (1969), Sampford (1962) and Freese (1962). Harris (1975) and Nie *et al.* (1975) were used for multivariate statistics. Detail will be provided later as appropriate. The following conventions and symbols will be used without further explanation:

$\bar{Y}$ = arithmetic mean

se = standard error (of the sample)

sem = standard error of the mean

ANOVA = analysis of variance

SV = source of variation

df = degrees of freedom

SS = sum of squares

MS = mean sum of squares

F = variance ratio

ns = not significant ($p > .05$)

* = $p < .05$

** = $p < .01$

*** = $p < .001$

t test = Student's t test

t′ test = Cochran's approximation of the Behrens-Fisher test (the approximate t test). Used where heterogeneity of sample variances is too great to meet the assumptions of the standard t test.

Lower case letters after $\bar{Y}$ or $\bar{Y} \pm$ se denote values significantly different ($p < .05$) based on Duncan's new multiple range test.

CHAPTER 2

POLYMORPHIC VARIATION OF LEAF SHAPE AND SIZE, AND THE CHROMOSOME NUMBER IN *H. PILOSELLA*

2.1 INTRODUCTION

In its native continent, Europe, *Hieracium pilosella* (subgenus *Pilosella)* is represented by a highly polymorphic polyploid apo-amphimictic complex (Gadella 1972, Sell and West 1976, Turesson and Turesson 1960). Although *H. praealtum* was found to be fairly constant between comparable habitats in the South Island, *H. pilosella* was frequently polymorphic. Since Turesson and Turesson (1960) found ecological differences between the chromosomal races of *H. pilosella* in Scandanavia, the primary aim of this study was to examine the populations in the Mackenzie Country and at Cave Stream used in growth, production and reproduction investigations (Chapter 3) for: (1) chromosomal race variation using a cytological technique and (2) major genotype differences underlying phenotypic variation of leaf shape and size by means of a transplant experiment. The scope of the investigation was expanded later to include a range of New Zealand populations of *H. pilosella* for comparison.

2.2 EXPERIMENTAL

Thirty-one collections (Fig. 2.1) of *H. pilosella* were obtained either as a single clone representative of the site or two or more distinct clonal forms from the same site taken for their distinctive appearance. Each collection

was separated into individual plants (see Chapter 3 for a definition of a hawkweed plant). Five plants per collection were grown singly in pots containing 900 cm^3 of a sandy loam. The plants were established in the Botany Department glasshouse (Christchurch) between August and November, 1978, and grown until April, 1979. At this time three leaves of post transplant ontogeny per plant (i.e., 15 per collection) were measured for length and width using vernier calipers. By growing the plants under uniform environmental conditions, phenotypic variation in the new growth between population samples was assumed to arise from genotypic differences (Clausen *et al.* 1948, Heywood 1967). Chromosome numbers were determined from root tip squashes after pre-treatment in monobromonaphthalene and staining in propionic orcein by the technique of Mahanty (1970) with three replicates.

Since all plants in each collection were from the same clone, the 15 measurements were treated as within plant variation. Two variables describing relative shape and size were derived as follows:

$$\text{Shape} = \log_e (\text{length} \div \text{width})$$

$$\text{Size} = \log_e (\text{length} \times \text{width})$$

2.3 RESULTS

The somatic chromosome number (2n) for all collections was 45. Wide variation in leaf shape and size (Fig. 2.2) unrelated to the sampling pattern (Fig. 2.1) persisted in the common (glasshouse) environment.

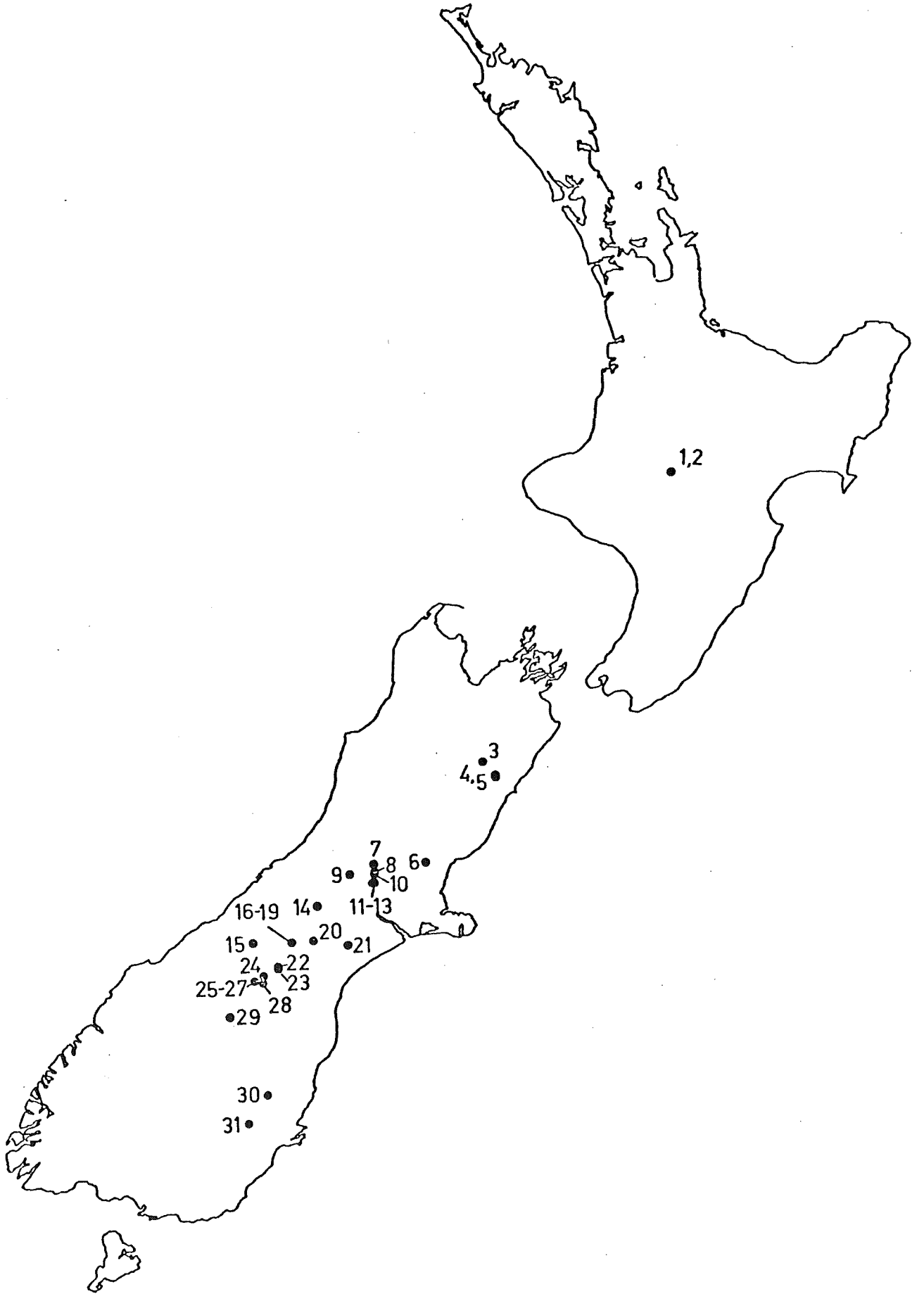


Figure 2.1 Distribution of collections of *H. pilosella*.

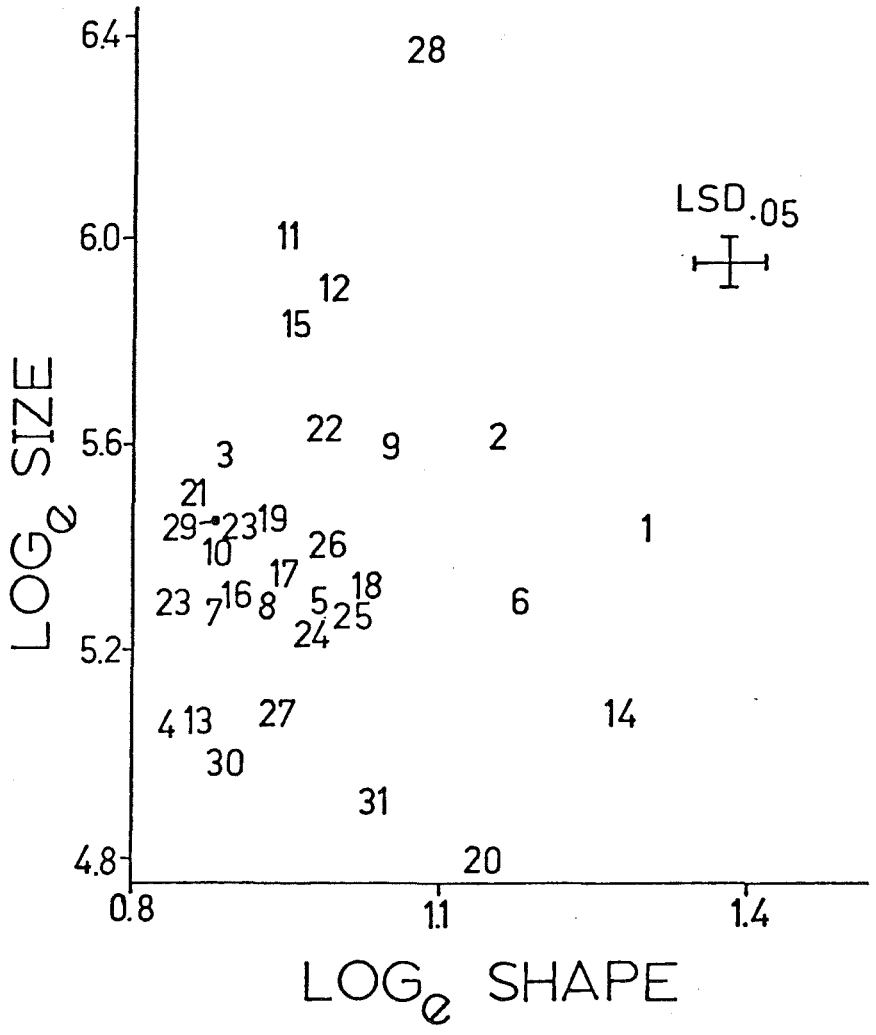


Figure 2.2 Variation in shape and size of *H. pilosella* leaves from plants grown in a common (glasshouse) environment from November 1978-April 1979. The collection numbers correspond to those given in Fig. 2.1.

2.4 DISCUSSION

The base chromosome number in subgenus *Pilosella* is 9 (Turesson and Turesson 1960). In Europe the diploid (2n = 18) and tetraploid (2n = 36) races are amphimictic, the triploids (2n = 27) are mostly sterile, and the higher ploidal races (mainly 2n = 45, 54 and 63) are usually facultative apomicts (*loc. cit*, Gadella 1972). From the 31 collections examined in this study, it seems likely that only a pentaploid (2n = 45) chromosomal race is present in *H. pilosella* in New Zealand. This finding has several implications.

In Europe, the different chromosomal races show geographical variation of their general distribution, morphological differences and habitat variation (Delcourt 1972, Gadella 1972, Turesson and Turesson 1960). The pentaploid chromosomal race generally occurs further north (Eire, Scotland, and through to northern Scandanavia) or in mountainous regions in southern Europe (*loc. cit*). The latitudes of the montane European distribution of the pentaploid race are comparable to those in the South Island. Therefore the New Zealand populations of *H. pilosella* are perhaps better adapted to the climate of the inland high country than that of the lower coastal regions where this species first established.

The pentaploid race occupied a wider range of habitats than other chromosomal races in Scandanavia (Turesson and Turesson 1960). This ecological amplitude is suggestive

of a "general purpose genotype" (Baker 1974) which accrues tolerance of abiotic environmental variation. Additionally the pentaploids produced longer scapes and stolons than other chromosomal races (Turesson and Turesson 1960). The latter superiority is particularly advantageous in spread from founder individuals in grazed grassland (Chapter 3).

A wide variation of forms, characteristic of the pentaploid chromosomal race (Turesson and Turesson 1960) of *H. pilosella*, was found in the transplant experiment. The extent of the differences which persisted in the common glasshouse environment indicates genotypic variation was present between some populations. However, no relationship was evident between the variation pattern and geographic location or major environmental conditions of the collection sites (Figs. 2.1, 2.2). It appears that, as in Europe, genetic variation introduced through amphimictic reproduction is being stabilised by apomixis and vegetative reproduction producing complex patterns of phenotypic variation. However compared with European descriptions (Sell and West 1976) *H. pilosella* is much less variable in New Zealand, both morphologically and chromosomally.

CHAPTER 3

GROWTH, REPRODUCTION AND PRODUCTION BIOLOGY OF *H. PILOSELLA* AND *H. PRAEALTUM*

3.1 INTRODUCTION

While some aspects of the biology and reproductive tactics of *Hieracium* species have been studied in North America and Britain (Bishop *et al.* 1978, Johnson and Thomas 1978, Reader 1978, Thomas 1972, Thomas and Dale 1974, 1975, 1976 , Yeung and Peterson 1972), minimal information is available on the principal New Zealand species, *H. pilosella* and *H. praealtum*. To objectively assess the weediness of these species requires specific information on growth patterns, production of dry matter, propagation (regeneration) and dispersal.

The first series of investigations described in this chapter refer to the seasonal phenology and growth characters of the species. It is contended that the success of perennial weeds on agricultural land is dependent, in part, on the effectiveness of vegetative reproduction (Raju *et al.* 1966). Initial field observations during 1974 in Canterbury high country at the start of this work strongly indicated that the importance of stolons relative to seed in the expansion of existing populations was high and seemed to be greater in *H. pilosella* than in *H. praealtum*. Differences in these two modes of regeneration imply dissimilarity of propagation and dispersal tactics, the fundamental regulators of the geographic pattern of colonisation and

population dynamics. These are described in more detail in the second series of investigations.

Definition of a hawkweed plant

Species with vegetative reproduction or clonal growth present difficulty delineating individual plants. In this study, a vegetative offspring that had established definite soil connections by roots immediately below itself was considered to be an independent plant. The establishment criterion was used in other hawkweed studies (Thomas 1972, Thomas and Dale 1974, 1975, 1976, Reader 1978). Even when the stolon did not subsequently whither and become non-functional, it was likely that transport of photosynthates, minerals and water between interconnected plants was negligible based on the findings for other clonal species (Dobinson 1977, Tietema 1979).

Growth analysis

There are two general approaches to determining the growth characteristics of species. The first approach, applicable for species occurring in nearly pure stands which is common in agricultural crop research, is to use direct harvest per unit area. The other approach is to measure attributes of the species and correlate them with dry matter production.

The degree of spatial heterogeneity in natural communities, in contrast to crops, is often sufficiently large to effectively prevent the selection of comparable stands needed in harvest clipping techniques for

determining a seasonal growth pattern. Based on the study of *H. floribundum* (Reader 1978), such techniques were considered unacceptable. Furthermore, in plant growth studies of natural communities it is often preferable to follow the growth of the same individual throughout the sampling interval. While indirect methods of growth analysis require calibration for biomass estimation, greater ease of field sampling and higher accuracy are often possible than with direct harvest techniques (Ondok 1971). Several workers have used indirect measures of growth (leaf extension, leaf appearance, etc.) on New Zealand flora with success (Mark 1965, Payton and Brasch 1978, Scott 1961, 1977 a,b).

3.2 STUDY SITES

The sites used in this study encompassed all but the driest of the soil-climate habitats under which *H. pilosella* and *H. praealtum* occurred. Most were in the Mackenzie Country but were also representative of other South Island high country areas.

The location of the sites is shown in Figs. 3.1 and 3.2. The geographic location and altitude were taken from the N.Z. Map Series 1, with the aspect, slope and other description of the topography determined on the site or from the general description of the area (O'Connor 1976). Soils on all sites were upland high country yellow-brown earths (N.Z. Soil Bureau 1968). The soil moisture classes and soil set names used below were those given by N.Z. Soil Bureau (*loc. cit.*). However most of the soils are

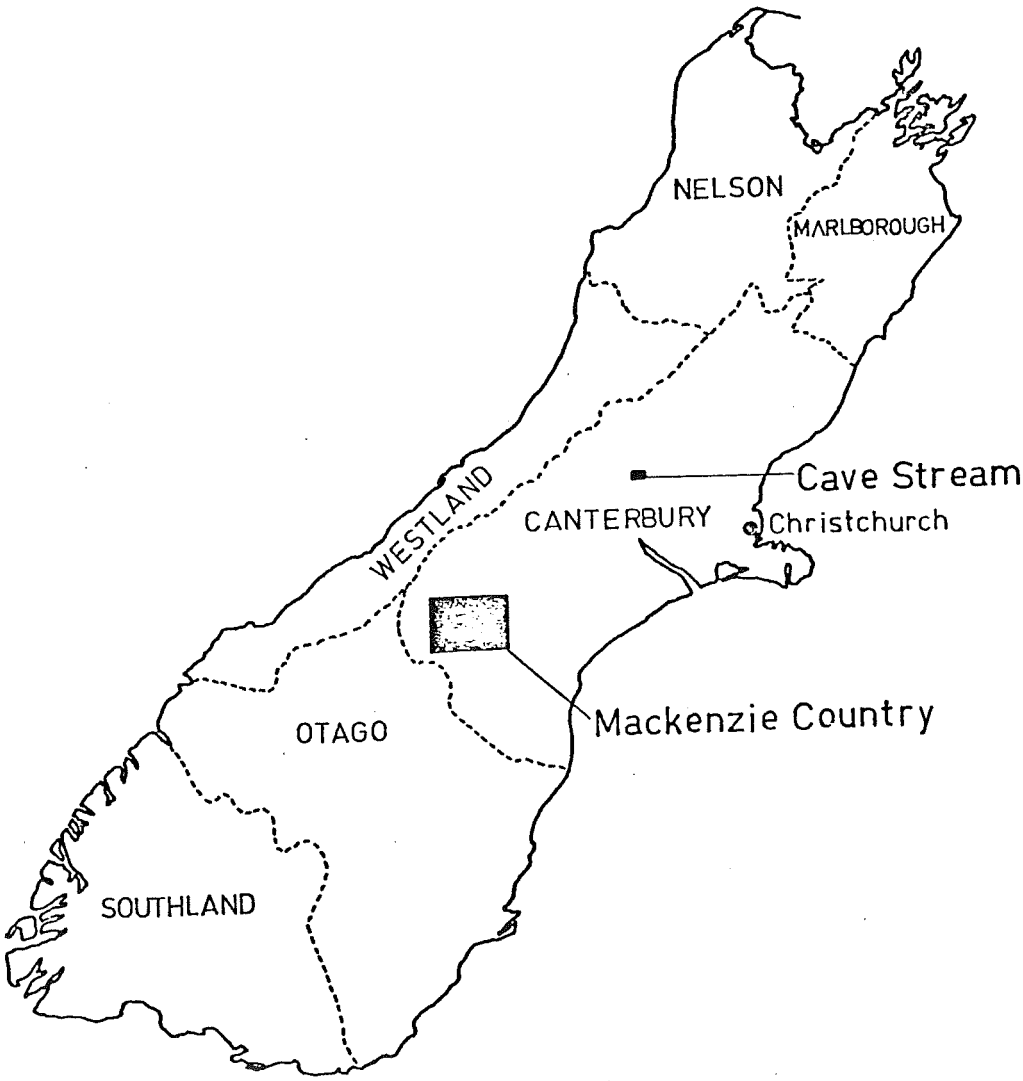


Figure 3.1 The study sites in the South Island, N.Z.

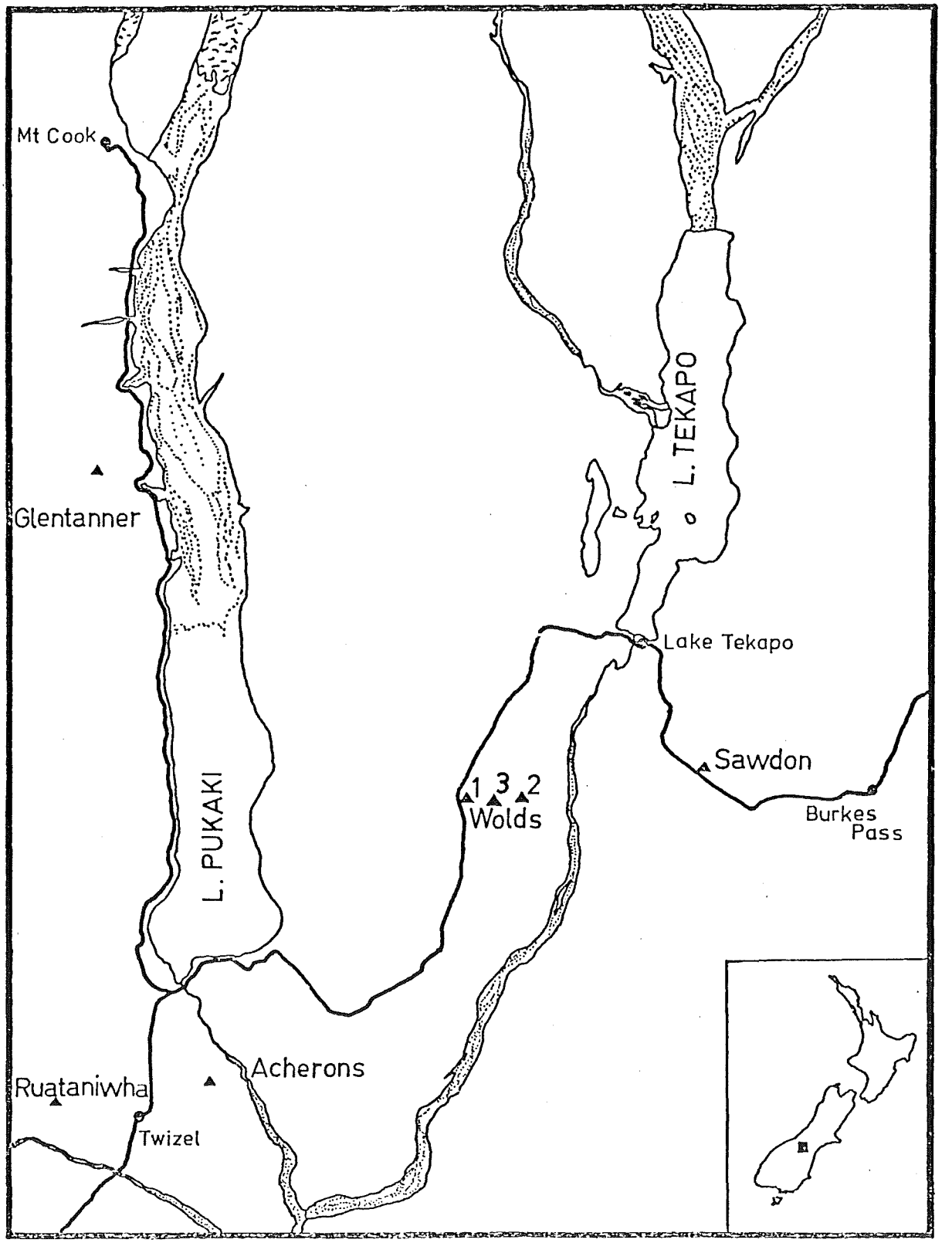


Figure 3.2 The six Mackenzie Country site locations.

being resurveyed (T. Webb pers. comm.) and the provisional soil type names have also been included.

All sites were tussock grassland (Connor 1964) and the most important species at each site is given. Detailed phytosociological studies of two of the sites will be given in Chapter 6.

The description of the sites is given below, listed in order of increasing moisture availability.

Site Name: ACHERONS

Location: S109/830695, 460 m a.s.l. SW aspect, <2° slope, 6 km south of Lake Pukaki on Ben Ohau Station.

Topography: Gently sloping glacial outwash plain with shallow soil overlying greywacke alluvium.

Soil: Shallow dry hygrous YBE. Glenbroock soil of Acheron set.

Vegetation: Dominated by *Festuca novae-zelandiae* with the other common species in approximate order of importance being *Hieracium praealtum, Rumex acetosella, Vulpia bromoides, Polytrichum juniperinum, Poa colensoi, Hieracium pilosella, Aira caryophyllea, Raoulia parkii, Hypochoeris radicata, Raoulia australis, Carex breviculmis, Carmichaelia monroi* and an occasional shrub of *C. petriei* and *Corallospartium crassicaule*.

Site: RUATANIWHA

Location: S109/727686, 500 m a.s.l. SE aspect, <2° slope, 2 km west of Twizel, and south of Mt.Ostler, on Ruataniwha Station.

Topography: Flat to undulating glacial moraine and outwash plain with shallow stony soil overlying greywacke alluvium.

Soil: Shallow dry hygrous YBE. Glenbroock soil of Acheron set. Soil slightly deeper than on Acheron site.

Vegetation: Dominated by *Festuca novae-zelandiae* with much bare ground, with other common species being *Hieracium praealtum, Erythranthera pumila, Rumex acetosella, Hypochoeris radicata, Hieracium pilosella, Aira caryophyllea, Vulpia bromoides, Raoulia parkii, Pimelea oreophila, Cyathodes fraseri, Luzula alophylla, Raoulia australis, Trifolium dubium, Vittadinia australis* and *Trifolium repens*.

Site Name: WOLDS 1

Location: S100/994877, 625 m a.s.l., SW aspect, $<2^{o}$ slope. East of State Highway 8, 800 m south of Irishman Creek on Wolds Station.

Topography: Flat, slightly easterly aspect of a deeper loess over outwash material.

Soil: Dry hygrous YBE, Wolds soil of the Pukaki set.

Vegetation: A modified fescue tussock grassland with very little bare ground. The common species were *Festuca novae-zelandiae, Poa pratensis, Bromus tectorum, Hieracium pilosella, H. praealtum, Rumex acetosella, Agrostis tenuis, Trifolium dubium, T. arvense, Carex breviculmis, Linum catharticum, Senecio hastii, Myosotis stricta* and *Veronica verna*.

This site was used for the growth and reproductive studies (this Chapter) because of the local abundance of the two *Hieracium* species and as it was also fenced.

Site Name: WOLDS 2

Location: S100/014875, 640 m a.s.l., level site, 2 km east of State Highway 8.

Topography: Level site on lateral moraine terrace.

Soil: Dry-hygrous YBE. Tekapo soil.

Vegetation: Fescue tussock - Matagouri grass-shrubland with little bare ground. The common species were *Festuca novae-zelandiae, Hieracium pilosella, Discaria toumatou, Agrostis tenuis, Carex colensoi, C. breviculmis, Coprosma petriei, Colobanthus brevisepalus* and *Anthoxanthum odoratum.*

The site was used for zonal reproductive variation and some half-life studies (Chapter 3), and soil nitrogen and phosphorus work (Chapter 4).

Site Name: WOLDS 3

Location: S100/006868, 615 m a.s.l. NW aspect, 2^{o} slope. 1 km east of State Highway 8, near the Wolds Station homestead.

Topography: Several slightly sloping stony terrace surfaces with shallow soil overlying greywacke alluvium.

Soil: Dry-hygrous YBE. Pukaki soil.

Vegetation: Barren weed community. The common species were *Hieracium pilosella, H. praealtum, Rumex acetosella, Raoulia australis, Aira caryophyllea, Agrostis tenuis, Carex breviculmis, C. colensoi* and *Luzula rufa.*

The site was used for estimating the proportion of seed versus stolon derived plants (Chapter 3).

Site Name: SAWDON

Location: S101/153895, 670 m a.s.l., $<2^{o}$ S slope, 200 m north of State Highway 8, south of Mt. Edwards and Mt. Burgess alongside Dead Man Creek on Sawdon Station.

Topography: Even outwash terrace

Soil: Deep dry hygrous YBE. Holbrook soil of the Pukaki set.

Vegetation: A fescue tussock grassland invaded by *Hieracium pilosella* (averaging c. 55% ground cover and up to 90% in places. The common species in approximate order of importance were *H. pilosella, Festuca novae-zelandiae, Agrostis tenuis, Coprosma petriei, Anthoxanthum odoratum, Pyrranthera exigua, Cyathodes fraseri, Rumex acetosella, Discaria toumatou, Trifolium dubium, Aira caryophyllea, Luzula rufa, Raoulia subsericea, Celmisia gracilenta, Deyeuxia avenoides, Stackhousia minima, Senecio hastii,* and *Aciphylla aurea. Hieracium praealtum* was rare on this site.

Site Name: CAVE STREAM

Location: S66/213973, 650 m a.s.l. 10^{o} NE slope. In the Broken River basin between the Torlesse and Craigieburn Ranges, 20 km NW of Springfield.

Topography: Sloping outwash terrace with shallow loess over shallow outwash material.

Soil: Shallow hygrous YBE. Craigieburn soil.

Vegetation: A grazed *Festuca novae-zelandiae* grassland with some large colonies of *H. pilosella, H. praealtum* and *H. lachenalii*. The other common species were *Agrostis tenuis, Discaria toumatou, Anthoxanthum odoratum, Verbascum thapsus, Erodium cicutarium, Rumex acetosella, Satureja acinos, Geranium sessiliflorum, Acaena caesiiglauca, Cyathodes fraseri, Hypochoeris radicata, Trifolium arvense, T. dubium, Pimelia oreophila, Luzula rufa* and *Aphanes microcarpa.*

Site Name: GLENTANNER

Location: S89/765094, 850 m a.s.l., level site, 200 m west of DSIR research station at Glentanner Station.

Topography: Level site on weathered lateral moraine terrace.

Soil: Hygrous YBE. Cass soil.

Vegetation: A *Festuca-novae zelandiae-Chionochloa rigida* grassland, partly modified by grazing but with almost complete ground cover. Both *Hieracium* species were minor species in the vegetation, with *H. praealtum* strongly restricted to bare ground at this elevation. The commoner species were *Racomitrium lanuginosum, Agrostis tenuis, Anthoxanthum odoratum, Gaultheria depressa, Hypochoeris radicata, Poa colensoi, Raoulia subsericea, Dracophyllum uniflorum, Cyathodes fraseri, Celmisia densiflora, Acaena caesiiglauca, Wahlenbergia albomarginata, Oreomyhrris colensoi, Lycopodium fastigiatum, Luzula rufa, Hebe odora, Gentiana corymbifera* and *Pimelea oreophila*.

The estimated precipation for the sites was obtained by interpolating the precipitation map for the Waitaki (O'Connor 1976 p.19) and is given in Table 3.1. Temperature recordings were made at the 5 cm soil depth using analogue chart recorders during the growth measurement experiment. Summaries are presented in Fig. 3.3 while the average for the main growth period October to February is given in Table 3.1.

The climatic summaries for temperature and precipitation relative to the long term normal for the N.Z. Meteorological Service Stations at the Hermitage, Lake Tekapo, and Tara

Table 3.1 Comparison of climate, soil fertility and soil depth of five Mackenzie Country sites.

Site	Annual precipitation (mm)	Temperature[1] (°C)	Soil Fertility	Soil Depth (m)
Acherons	475	19.3	medium	0.3
Ruataniwha	600	18.4	medium	0.4
Wolds 1	675	18.3	low-med.	0.8
Sawdon	800	17.8	low	1.0
Glentanner	1300	16.4	v. low	0.3

[1] Average October 1978 - February 1979.

Table 3.2 Chemical analyses of the 0 - 7.5 cm soil depth at the Mackenzie Country sites (MAF-Invermay)

Nutrient			Site				
	Units	Soil:Soln	Acherons	Ruataniwha	Wolds 1	Sawdon	Glentanner
pH		1:2.5	5.1	5.2	5.3	5.3	4.8
P	ppm Olsen	1:50	24	24	16	12	8
Ca	pp 40,000	1:5	2	3	6	7	3
K	pp 250,000	1:5	5	5	11	9	5
Mg	pp in solution	1:5	5	7	21	29	10
C	%	-	2.1	2.9	3.4	4.1	5.3
N	%	-	.09	.11	.12	.12	.12
C:N		-	23	26	28	34	44
S	mg SO_4/ml soil	1:5	3	3	3	4	5

Table 3.3 ANOVA of seed production (seed plant^{-1}) and stolon production (cm plant^{-1}) under field and glasshouse conditions.

Source of variation	Seed production			Stolon production		
	df	MS	F	df	MS	F
Species	2	58.4	1688***	1	44.2	170***
Location	1	50.2	1450***	1	11.4	44***
S x L	2	9.4	270***	1	5.2	20***
Error	99	.035		66	0.26	

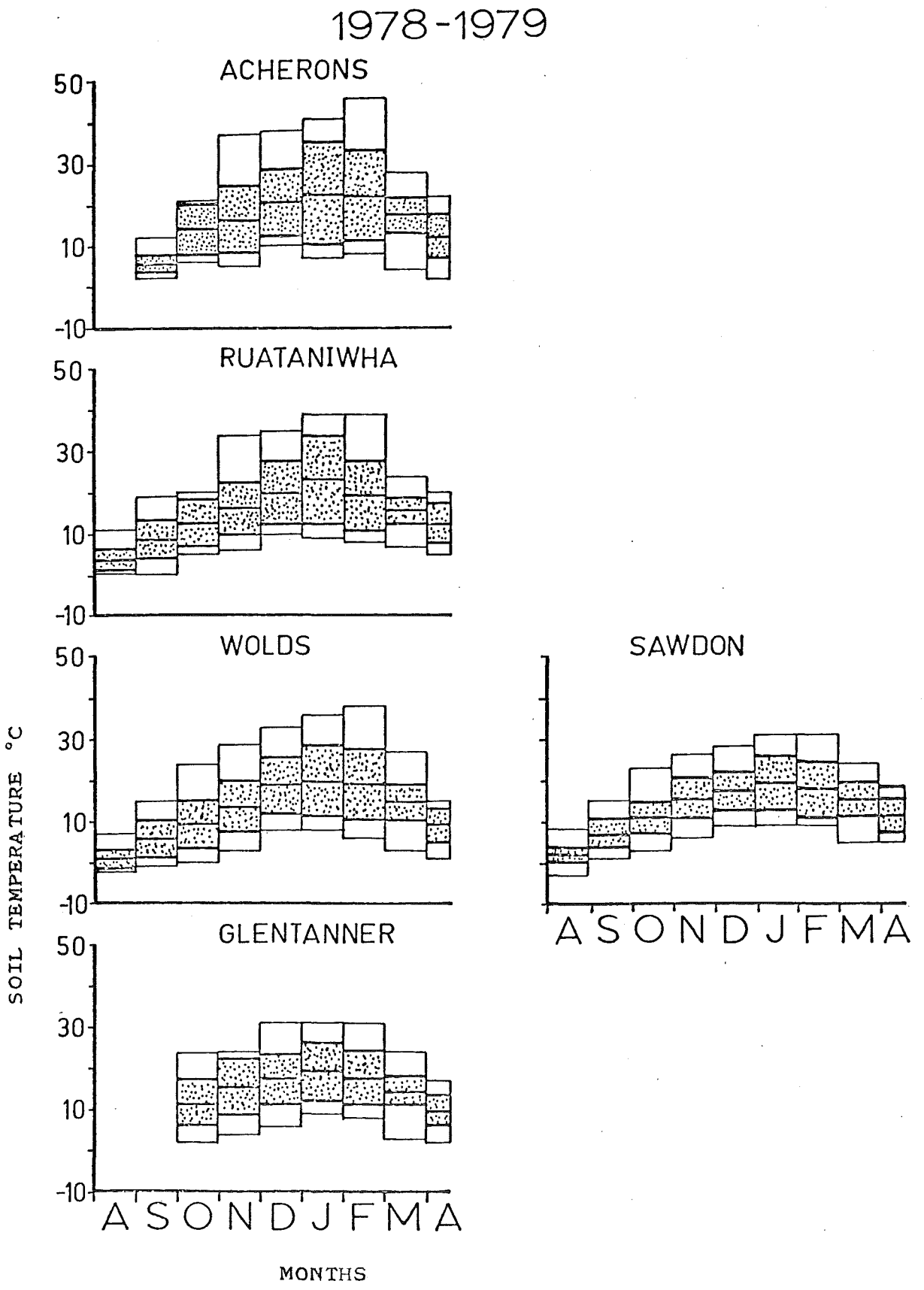


Figure 3.3 Monthly soil temperatures at the Mackenzie Country sites showing mean, mean maximum and minimum and extremes at the 0.05 m depth.

Hills are presented in Appendix A. During the major *Hieracium* growth measurement from August 1978 to May 1979 the main deviations from normal were; the end of winter was warmer and wetter; January (mid summer) was drier; and March (early autumn) was wetter.

The relative soil fertilities of the Mackenzie Country sites wereobtained from bulked samples consisting of 15 cores taken from the surface 7.5 cm layer between 10-12 January, 1979, and analysed by the M.A.F., Invermay (Table 3.2).

These show that available phosphorus varied inversely with the annual rainfall. Similarly, total carbon, sulphate and C:N ratio were related (directly) to precipitation. The highest base status (Ca, K, Mg) was determined from intermediate sites in the series (Wolds 1 and Sawdon). The pH was somewhat variable between sites and lowest at the wettest site (Glentanner). Table 3.1 summarises the important differences between the five Mackenzie Country sites. The sites are ordered in terms of increasing moisture availability. Declining moisture is accompanied by increasing temperature. Since water is the principal limiting factor to plant growth in the Basin (O'Connor 1976), the precipitation decrease and temperature rise from the northwestern sector to the central region represents stress attenuation. These climatic processes and variations are reflected by the fertility of the soils in the region. Central sites (e.g. Acherons, Ruataniwa) were more naturally fertile overall, although sulphur deficient because of low atmospheric return (O'Connor 1976),

relative to sites nearer the moist perimeter (e.g. Glentanner, Sawdon). Phosphorus deficiency and C:N ratios increased to very limiting levels with higher precipitation.

Most of the climatic range of *H. pilosella* and *H. praealtum* appeared to be found within the site series. At one extreme, the Acherons site was a stress site; low rainfall, high temperature, shallow, well drained soil (i.e. poor moisture retention) although relatively fertile. At the other end of the scale, the Glentanner site had the minimum stress level of the series but was probably limiting in terms of low fertility, low temperatures during the early part of the growing season (unmeasured until the end of snow lie) and mountain shadow effects (e.g. shorter insolation periods). Although at lower altitude, the Sawdon site was affected by low prevailing temperatures (two periods of snow lie 3 and 9 days duration after August 1978). Among these sites, the Wolds 1 represents conditions which are a favourable compromise of water availability (precipitation, soil storage), temperature and fertility in terms of plant growth.

3.3 EXPERIMENTAL

Initial species comparison

The first comparison of *Hieracium pilosella, H. praealtum* and *H. lachenalii* was made with adult plants collected from the Cave Stream site in May 1975, transplanted singly into 13 cm diameter pots containing 700 cm^3 of coarse sand: loam (1:1), and grown in a glasshouse at the Botany Department (air temperature maintained above 8^{o})

until May 1976. Measurements were made of the length of stolons formed and capitulas were collected to determine seed output of Cave Stream re-producing plants in the field (n = 25 plants/species) and glasshouse (n = 10 plants/species) by counting achene positions using a binocular microscope. Average seed number and total stolon length per plant were analysed after transformation of variates to $\log_e$.

Leaf, inflorescence and stolon production

The growth patterns of *Hieracium pilosella* and *H. praealtum* at the five Mackenzie Country sites were determined at 2-4 weekly intervals from 1 August 1978 to 17 April 1979. One hundred plants per species per site were selected at the start using a randomised grid procedure and plants identified with a small metal numbered tag in the soil. The leaf apex of the youngest emergent leaf was marked with a spot of artists' oil paint at each sampling with different colours being used to identify marking dates. The number of new leaves which appeared between samplings was counted.

Inflorescence development was followed by defining and recording four (ordinal) growth stages as follows:

(1) inflorescence formed but no scape,

(2) scape extended to approximately half final height,

(3) scape extended to near full height and inflorescence(s) in flower, and

(4) scape and inflorescences at peak development.

Type specimens were kept for maintaining consistency in assigning stages.

Capitulas were collected after seed had dispersed

and seed produced was determined by counting attachment points under a low power (15x) binocular microscope.

Stolons were counted and length from parent plant measured.

Double sampling: dry matter relationships

In addition to the measurements of indirect growth indices on the marked plants, the same measurements were made on comparable plants harvested for dry matter, termed a parallel harvest. This technique, known as double sampling (see Freese 1962), enables the greater part of the sampling effort to be directed towards collecting the larger primary sample of indirect growth values. The main drawback is the extensive statistics required to integrate the two separate procedures.

Successive parallel harvests (n = 10 species^{-1} site^{-1}) were made of leaves, inflorescences and stolons at growth increments (1 leaf, 2 leaf, ... nth leaf). Daughter plants grew very rapidly so direct harvests were used for these parts. Harvests were kept in sealed plastic bags at low temperatures (< 4^{o}C) for periods varying from 8-72 h before returning to the laboratory for drying at 80^{o}C to constant weight (usually 3 days).

Double sampling: production estimates

The weight of new growth was estimated by multiplying weight per plant part by density and by the factor for multiple parts (stolons, daughters) obtained from the primary sample. It was assumed, and supported by observations, that

a reproductive parent vacated its place in the patch to be replaced by a vegetative offspring. This proportion determined the contribution vegetative offspring made to the new growth. The additional area occupied based on the number of daughters which survived to late autumn less replacement was used to express stolon weight on a density basis and calculate rates of spread in area.

Double sampling: statistics

The precision of the double sampling procedure is based on the sample size of the larger primary sample (Sampford 1962). The variance estimates of the combined double samplings were produced using the rules for ratios of propagation of error with covariance (Freese 1962 p.18).

The conversion of indirect growth values with interval scale properties (leaf appearance, stolon length) was achieved with regression estimation double sampling procedures. Freese (1962) presents the basic techniques. The more advanced statistics required for variance estimates, when double sampling, are given by Sampford (1962). Empirical curve fitting techniques were used which only require that fitted curves must describe the data adequately and that these data are a satisfactory representation of the growth process (see Hunt 1978 p.41).

Weights of the secondary samples were transformed ($\log_e$) to equalise variances so that the error mean square term could be used as an estimator of variance for the whole curve. Successive polynomials were fitted stepwise introducing linear, quadratic and cubic terms with only

the significant terms used.

From Samford (1964 p.137) the variance of the mean is:

$$\frac{Se^2}{n2}\left(1 + \frac{1}{n2}\right)\left(1 - \frac{n2}{n1}\right) + \frac{Sy^2}{n1}\left(1 - \frac{n1}{N}\right)$$

Se^2 and Sy^2 were obtained from the regression of the secondary sample weight on the growth index; Se^2 corresponds to the deviations from the regression MS, Sy^2 is the variance or total MS, n1 = the primary sample of 100, and n2 = the total number of observations in the secondary sample.

For ordinal measurements (inflorescent stage, stolon number), the average weight at each sampling is given by the formula:

$$W_I = I_1 . W_1 + I_2 . W_2 + I_3 . W_3 + I_4 . W_4$$

where I = number of inflorescences at the stage indicated by the subscript,

W = the weight at the stage given by the subscript (n = 10).

The variance of the mean is estimated using the rules for propagation of errors for a sum (Freese 1962 p.18) as follows:

$$S^2_{WI} = n_1^2 . S_1^2 + n_2^2 . S_2^2 + \ldots\ldots n_4^2 S_4^2$$

where n = number of inflorescences/scapes at the stage denoted by a subscript

S^2 = variance of the subsample at the stage denoted by a subscript.

Net primary production

The net aerial production was estimated as the difference between new growth at the peak summer biomass and the starting weight of over-wintered living shoot material (based on 100 plants species^{-1} site^{-1} collected in the beginning of August 1978 before growth commenced). The maximum living biomass was taken to have occurred at the peak of seeding (see Tietema and Vroman 1978). The maximum living biomass was derived from the growth curve as the sum of the leaves remaining (non-reproductive plants weight), inflorescences and scapes, and the stolons. The January sample was used for all cases except Sawdon where February was used since seeding was late there. The calculated values were adjusted for the maximum vegetation cover attained by resident species.

Zonal variation in colonies

Marked variation of plant size, stolon number and length and seed production was evident only in the more extensive colonies of *H. pilosella*. Some of these characteristics in *H. pilosella* patches were quantified for comparison at Wolds site 2. The density (plants/dm^2, n = 30) reproduction frequency (proportion of plants reproducing n = 30) seed production (n = 50) and total stolon length (n = 75) for reproducing plants located in the dense central and expanding outer regions of several patches were sampled as described earlier.

Other measurements

The density of plants within the marked patches was obtained from counts within 30 1 dm^2 quadrats which included the marked plants. Being a census, the variability within each species - site group was not included in the error estimation when the plant weights were adjusted to a unit area basis.

Root:shoot ratios were made on a single occasion (December 20-24 1978) from washing out 30 plants per species per site.

At the Wolds 3 and Ruataniwha sites 5 000 plants were sampled for their occurrence as single plants or as multiple colonies.

Light grazing sufficient to top the uppermost shoot parts (inflorescences and scapes) was simulated by fortnightly removal of these parts by hand from reproducing plants of *H. pilosella* and *H. praealtum* at the Wolds site 1. The total length and number of stolons formed at the end of the stolon growth period (mid February) were measured, counted, and the values obtained adjusted for plant density.

3.4 RESULTS

Initial species comparison

Analysis of the comparison of *Hieracium pilosella*, *H. praealtum* and *H. lachenalii* from the Cave Stream site showed there were significant differences in stolon length and numbers of seed as related to species, source of material and the interaction between the two (Fig. 3.4,

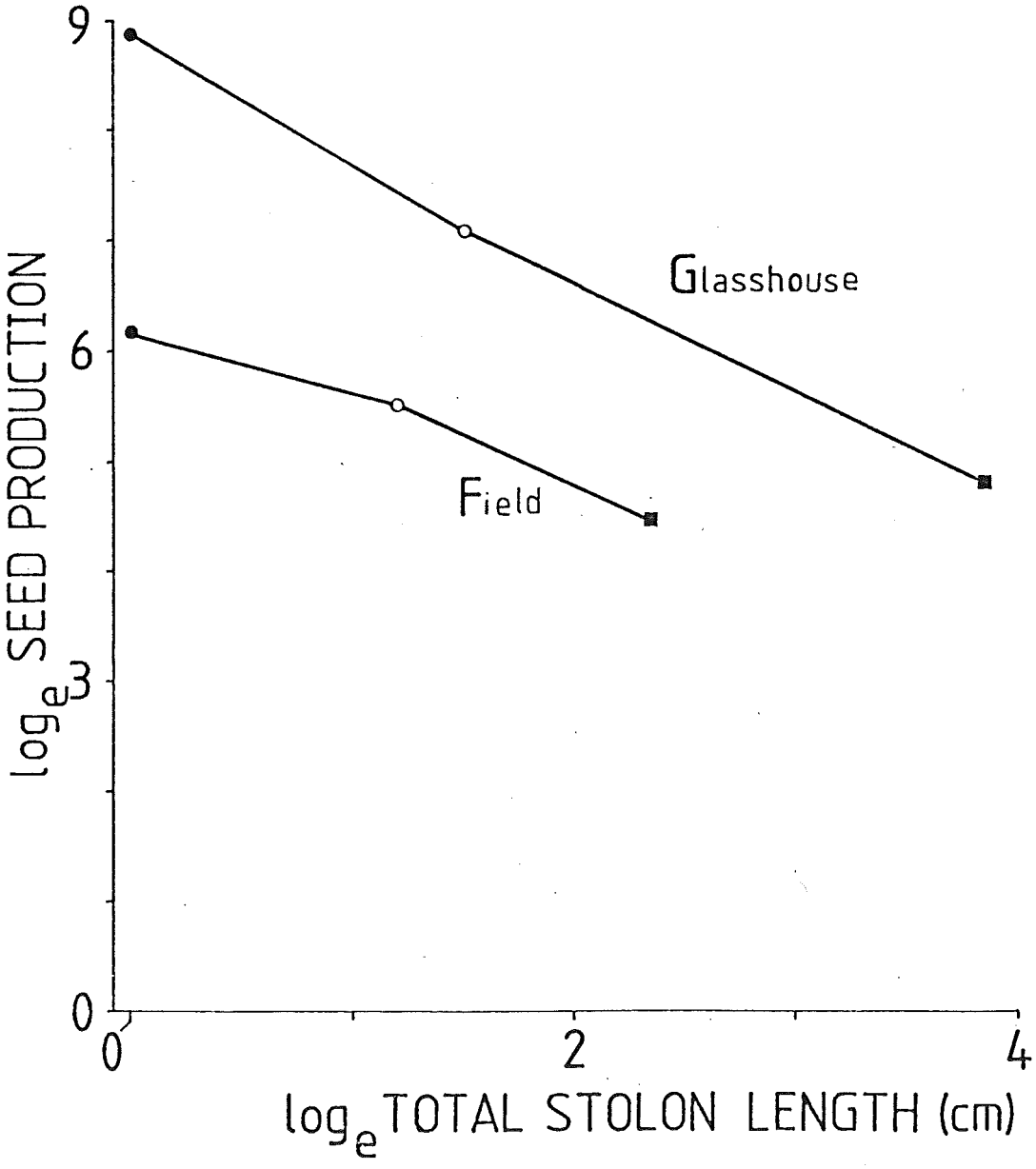


Figure 3.4 Relationship between seed output and stolon formation for *Hieracium lachenalii* (●), *H. praealtum* (o) and *H. pilosella* (■) at Cave Stream and in the glasshouse.

Table 3.3).

The species with high seed production (*H. lachenalii* and *H. praealtum*) or long stolons (*H. pilosella*) were limited relatively more by stress (i.e. field conditions *cf.* glasshouse conditions) than species with inferior seed production or stolon formation. However, over the range of conditions used in this experiment, the three hawkweeds maintained certain characteristic traits. *H. pilosella* was a highly stoloniferous, low seed production species whereas *H. lachenalii* was non-stoloniferous (although apparently with a rhizomatous capacity, see Dunbar 1977), but a copious seed producer. These attributes in *H. praealtum* were intermediate. The significant interaction relates to the inverse relationship between seed production and the length of stolons formed, which held for both sets of conditions (Fig. 3.4).

Phenology

From observations at 2 - 4 weekly intervals over four growth seasons the following is the growth and reproductive pattern in *H. pilosella* and *H. praealtum*. Many of these points will be quantified in later sections. The appearance of new bright-green leaves in the centre of reddish-green leaves of the overwintering rosettes began during early August. Leaves produced early or very late in the growing season were smaller than those produced in the main growth period from mid spring to early summer.

Inflorescences and stolons were initiated about November. No plant produced stolons without at least initiating inflorescences. Scape development and flowering

occurred about one to three weeks later and seemed to depend upon favourable soil moisture levels. Inflorescence abortion was evident during dry periods and was frequent among plants which had late inflorescence initiation. Rapid scape development and flowering, within as little as one day, was evident in *H. pilosella*, apparently because development of the inflorescence was already accomplished while near the rosette. The multiple inflorescence of *H. praealtum* took more time to reach full height and maturity. The inflorescences matured in a basipetal sequence from the oldest (terminal) back through the youngest (lateral) ones.

Flowering was completed in *H. praealtum* about two to three weeks earlier than *H. pilosella*. Seed of both species appeared from December to mid January and was dispersed by wind within days of seed maturity except when still air weather prevailed.

Stolons grew rapidly outward from the parent plant after initiation in November. The stolons of *H. pilosella* were thin and grew through close grazed vegetation, escaping grazing sheep to a considerable degree. *H. praealtum* stolons arched upward initially and appeared accessible to sheep grazing. Roots produced at leaf nodes along the length of stolons of both species anchored them close to the soil. After this had occurred, *H. praealtum* stolons were much less prone to grazing damage than before.

A single daughter plant appeared at the distal end of each stolon. These vegetative progency rooted about February after rainy periods when stolon elongation stopped. Daughter plants occupied space either formerly held by

parent plants in the patch, which had become leafless at this stage, but mainly in the surrounding area (vegetation or bare ground) thereby extending the colony. In this way, a dense advancing front was produced with gaps in the inner region being filled when they occurred. On very dry shallow soils, a bare central region appeared which was not re-colonised.

It is re-emphasized that plants which reproduced subsequently died, so that there is a large annual turnover of plants.

Seasonal growth patterns

Leaf, inflorescence and stolon production.

The estimated seasonal growth patterns of leaf, inflorescence and stolon production, determined from the periodic double sampling technique described, are given in Fig. 3.5. Primary data is in Appendix B.

The seasonal pattern is best illustrated by the highly reproductive populations at the Wolds 1 site. Four phenological stages occurred:

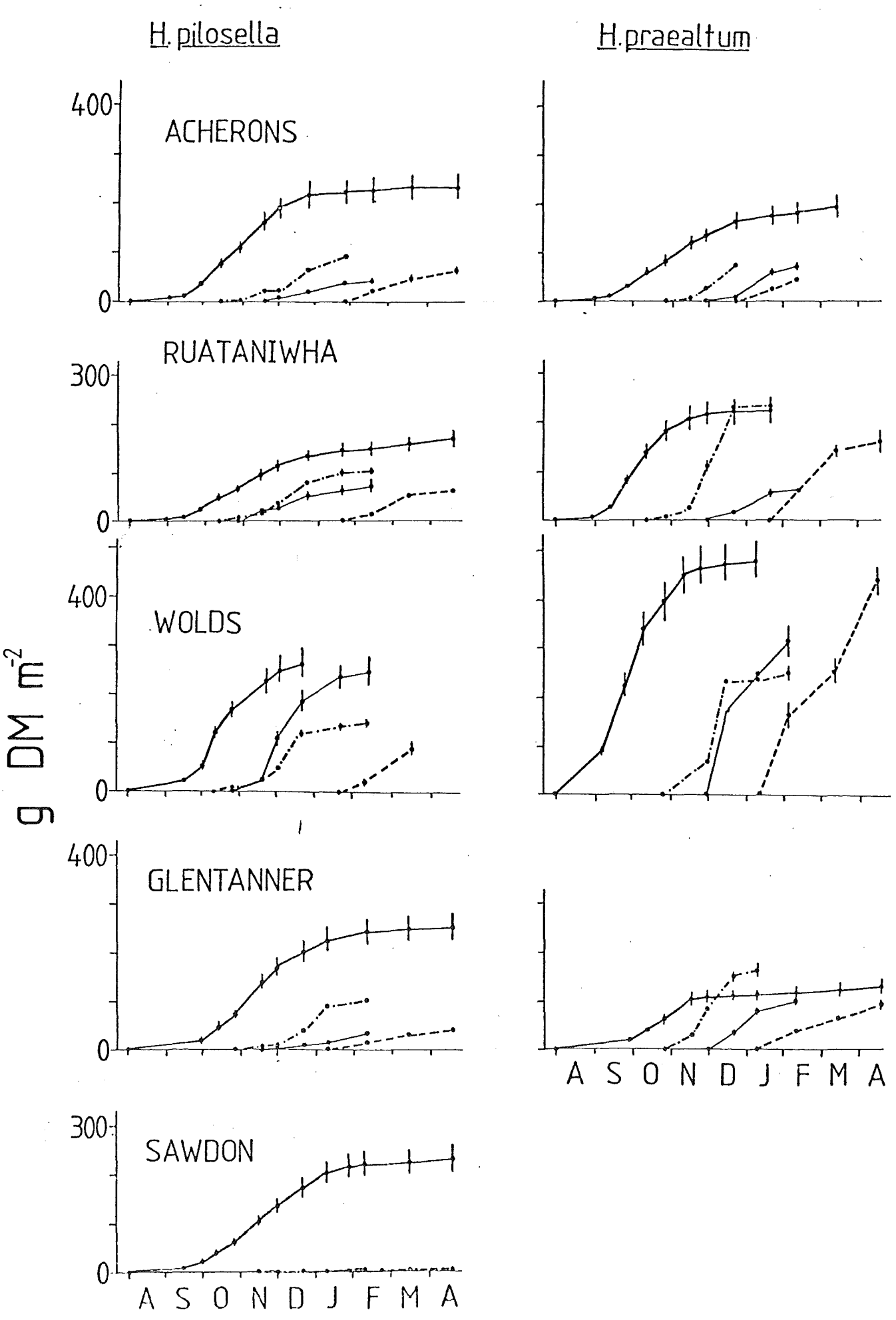
(1) new leaf growth of overwintering plants from August to mid November,

(2) inflorescence growth starting,

(3) stolon elongation beginning, and

(4) vegetative offspring growth.

Phases (2) and (3) occur about the same time. The transition of growth from phase (1) to (2) and (3) to (4) is masked in less reproductive populations where (1) may continue for most or all of the growth period.


H. pilosella
H. praealtum
ACHERONS
RUATANIWHA
WOLDS
GLENTANNER
SAWDON
400
300
0
g DM m-2
A S O N D J F M A

At three of the four comparison sites, Ruataniwha, Wolds 1, and Glentanner, *H. praealtum* leaf growth is greater and completed more rapidly than in *H. pilosella*. After reproduction and establishment of vegetative progeny , a second period of new leaf growth from the daughter plants occurred. At the Acherons, *H. praealtum* performed poorly in amount and rate of new leaf growth by comparison with its performance relative to *H. pilosella* at the other sites. The lower spring temperatures at Glentanner and Sawdon were reflected in the lower growth of leaves during that period.

Inflorescence growth for both species followed the pattern of the amount of leaf growth. It was greater for *H. praealtum* at the moister sites (Glentanner, Ruataniwha and Wolds 1) but inferior to *H. pilosella* inflorescence growth at the Acherons site.

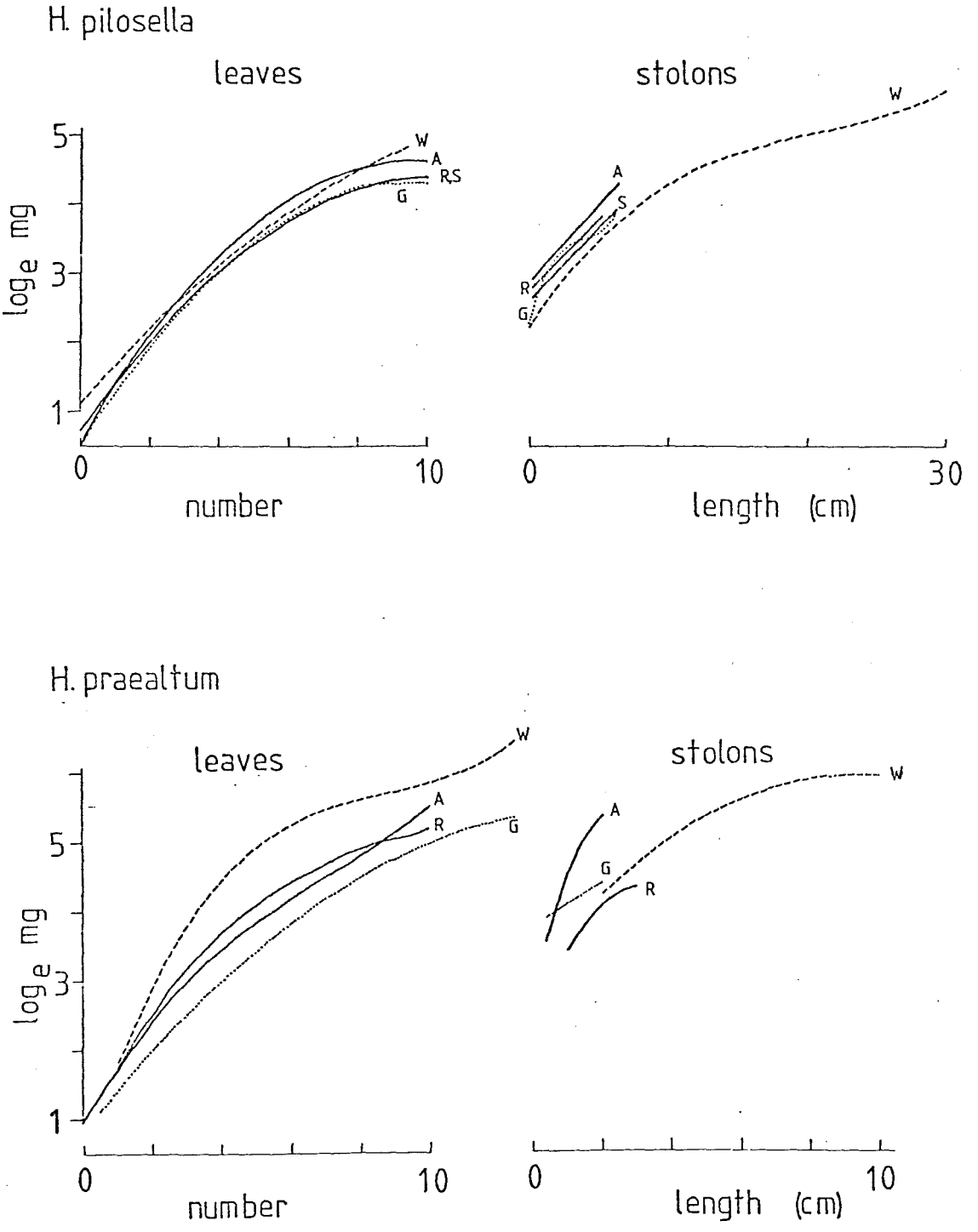
Slightly more stolon growth was measured for *H. praealtum* than *H. pilosella* at the moister sites (Glentanner, Ruataniwha and Wolds 1), but it was inferior to *H. pilosella* stolon growth at the Acherons site. Subsequent growth from daughters was greater for *H. praealtum* everywhere.

Dry matter relationships.

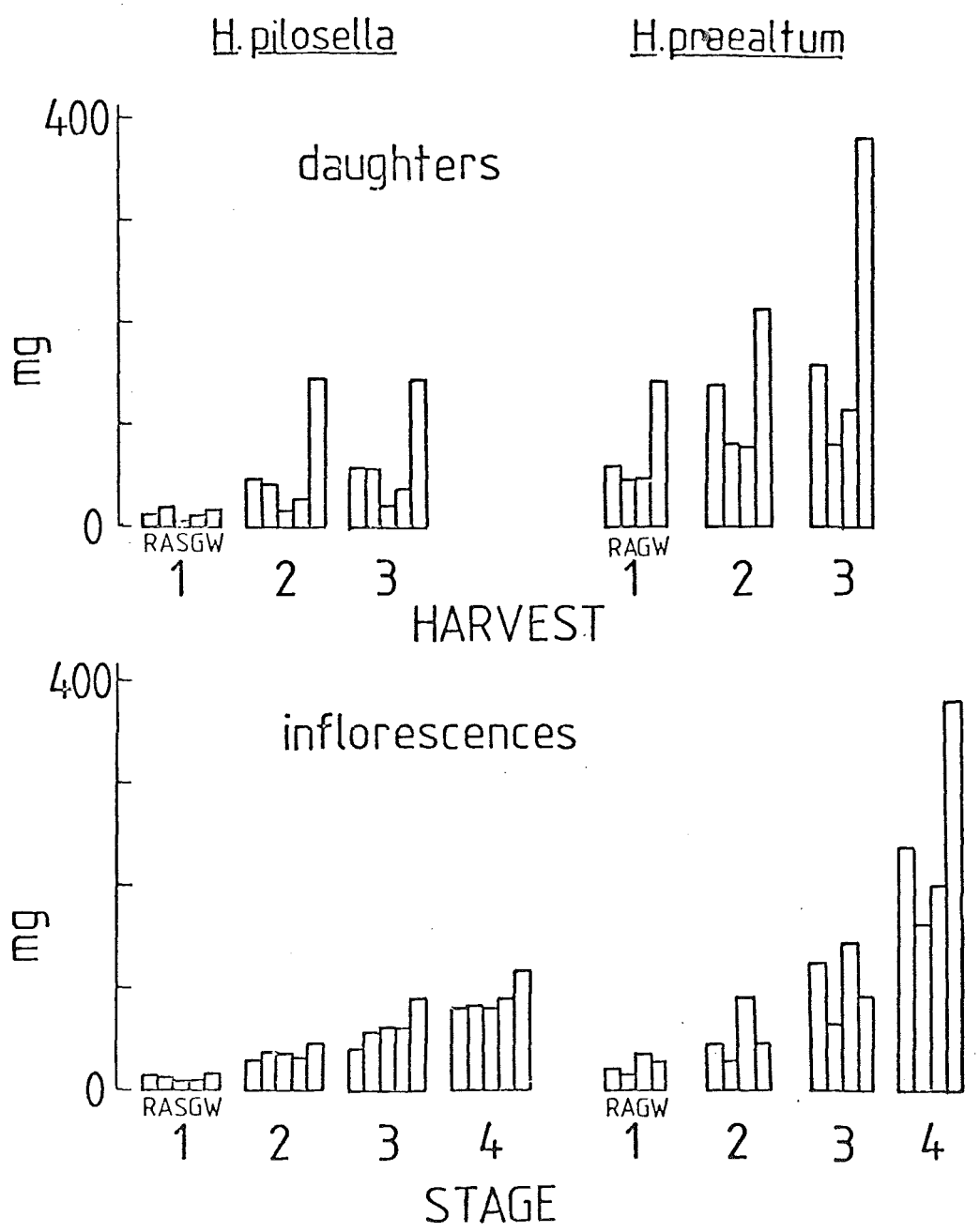
The dry matter relationships used in converting the indirect growth indices to estimated dry matter growth in the previous section are given in Fig. 3.6, with the statistics in Appendix B.

These relationships show that *H. praealtum* was a much more variable species than *H. pilosella* with respect to macroenvironmental variation as shown by the

(a)


H. pilosella
leaves
stolons
W
A
R,S
G
S
R
5
3
1
$\log_e$ mg
0
10
number
30
length (cm)
H. praealtum
leaves
stolons
W
A
R
G
5
3
1
$\log_e$ mg
0
10
number
length (cm)

(b)


H. pilosella
H. praealtum
400
daughters
mg
0
RASGW
RAGW
1
2
3
HARVEST
400
inflorescences
mg
0
RASGW
RAGW
1
2
3
4
STAGE

near identical leaf number to plant weight relationships for *H. pilosella* from the different sites. By contrast the weight per stolon length decreased from the driest (Acherons) to moister sites. The range of values again shows the higher stolon production from the Wolds 1 site.

The leaf number to plant weight relationship varied between the sites for *H. praealtum* and was not related to the environmental gradient. The stolon length to weight relationship was highest for the Acherons site.

Root-shoot ratios.

Root-shoot ratios were lower for *H. pilosella* at each site except Glentanner (Table 3.4). If these ratios are interpretated as how much root biomass is necessary to support the shoot system, then ecological performance in relation to the climatic-edaphic gradient can be assessed. *H. praealtum* root-shoot ratios increased with decreasing precipitation with a sharp increase at the driest site. *H. pilosella* root-shoot ratios were lowest at the intermediate Wolds 1 site and rose towards both extremes of the site series. *H. pilosella* had broader ecological amplitude with the optimum located near the central sites while *H. praealtum* was better in the wetter conditions.

Net primary production

The net aerial primary production (excluding herbivore predation which was insignificant) was 2.8 times greater for *H. praealtum* than *H. pilosella* at the moister sites (mean of

Table 3.4 Root to shoot ratios for *H. pilosella* and *H. praealtum* at five Mackenzie Country sites (n = 30)

Site	*H. pilosella*	*H. praealtum*	t test
Acherons	1.3 ± 0.4	2.4 ± 0.6	8.4***
Ruataniwha	1.0 ± 0.3	1.3 ± 0.4	3.3**
Wolds 1	0.4 ± 0.6	0.8 ± 0.4	3.0**
Sawdon	0.8 ± 0.4		
Glentanner	1.0 ± 0.4	0.7 ± 0.2	3.6**

Table 3.5 Net aerial primary production of *H. pilosella* and *H. praealtum* at five Mackenzie Country sites Values g m^{-2} $annum^{-1}$.

Site	*H. pilosella*	*H. praealtum*
Acherons	10	6
Ruataniwha	13	49
Wolds 1	50	135
Sawdon	1	-
Glentanner	12	27

Table 3.6 Percentage of seed-derived individuals at Wolds 1 and Ruataniwha sites (n = 5000)

Site	*H. pilosella*	*H. praealtum*
Wolds	1.0	6.8
Ruataniwha	0.9	0.9

Glentanner, Wolds 1, Ruataniwha; no comparison at Sawdon) (Table 3.5). At the driest site (Acherons) *H. pilosella* was the more productive species. The Sawdon production (*H. pilosella* only) was extremely low. Considering that 80% of the vegetation was comprised of this species, the production by this community was severely reduced compared with the level attained with pasture species or even low fertility resident species like *Agrostis tenuis* on this site. The potential production with moderate fertiliser (200 kg ha Mo Superphosphate 200S) is likely to be 300-400 g m^{-2} $annum^{-1}$ (Scott 1979).

Regenerative biology

Seed derived-plants.

The relative contribution of seed- and stolon-derived progeny to the maintenance of populations of *H. pilosella* and *H. praealtum* was estimated from the number of single plants relative to the number in colonies of various size. At the Wolds 1 and Ruataniwha sites on shallow soils a large group of discrete colonies of both species occurred with sizes ranged from pioneer individuals and small groups through to large degenerating (*sensu* Watt 1947, i.e. with a non-vigorous or dead central region) colonies. Consequently it was assumed that these populations were probably in a balanced state in terms of recruitments and losses. Examination of these populations and others during 1976 - 1979 did not reveal evidence of seedling establishment within a colony despite ephemeral seedlings seen briefly during wet periods. A similar lack of seed establishment within existing colonies

was found for Canadian *H. floribundum* populations (Yeung and Peterson 1972). Hence the number of single plants relative to those in colonies of two or more plants is a highly probable measure of the proportion of plants established from seed in the population.

A census showed seed was of relatively minor importance in contributing new plants to the populations of *H. pilosella* and *H. praealtum* at these two sites (Table 3.6). At the Wolds 1 site, seed was more important to *H. praealtum* than *H. pilosella*. However, at Ruataniwha where conditions were less favourable to germination and establishment, both species had equal proportions of seed-derived individuals.

Stolon and seed production

From the seasonal growth measurements the comparative regenerative potential of the two species is presented in Table 3.7. *H. praealtum* produced more seed per unit area than *H. pilosella* except at the driest site (Acherons) where it was inferior. Inflorescence abortion was slight (< 10%) at all sites except the Wolds 1 (Table 3.8). The higher incidence (c. 30%) might be the result of a two week dry spell, during an otherwise moist period, coinciding with inflorescence development at this site.

H. pilosella produced more stolons of greater total length than *H. praealtum* at all sites although the differences for Ruataniwha stolon production and Glentanner stolon length were not significantly different ($p = .05$). Mortality of new plants between summer and late autumn was greater for

Table 3.7 Comparative seed and stolon production of *H. pilosella* and *H. praealtum* at five sites during 1978/79 season.

	H. pilosella	*H. praealtum*	*t'* test
(a) Seed production (No. dm^{-2})			
Acherons 43/42[1]	790 ± 220	580 + 290	3.9 ***
Ruataniwha 47/73	910 ± 360	2690 ± 1110	10.6 ***
Wolds 1 52/64	1340 ± 630	1880 ± 890	3.7***
Sawdon 2/ -	30	-	-
Glentanner 33/87	810 ± 230	1510 ± 630	8.9***
(b) Stolon production (No. dm^{-2})			
Acherons 40/36	16 ± 7	6 ± 2	8.7***
Ruataniwha 49/77	22 ± 9	20 ± 9	1.2 ns
Wolds 1 78/95	44 ± 17	36 ± 13	3.4***
Sawdon 3/ -	2 ± 1	-	-
Glentanner 33/91	18 ± 7	15 ± 6	2.6*
(c) Total stolon length (cm dm^{-2})			
Acherons 40/36	32 ± 39	7 ± 5	4.0***
Ruataniwha 49/77	97 ± 105	28 ± 32	4.5***
Wolds 1 78/95	544 ± 358	172 ± 105	8.9***
Sawdon 3/ -	2 ± 2	-	-
Glentanner 33/91	30 ± 35	18 ± 17	1.9 ns

[1] Sample size for *H. pilosella* and *H. praealtum* respectively.

Table 3.8 Estimated population dynamics of *H. pilosella* and *H. praealtum* at five sites during 1978/79 season. Per 100 spring plants.

Reproductive = overwintering plants which become reproductive and subsequently die (loss)

Abort = flowers which abort before seeding

New daughters = new daughters produced in mid summer (gain)

Autumn mort. = autumn mortality of new daughter plants (loss)

% survival = % of daughters which survive into autumn

Nett = net change late winter to autumn

$$\text{Half-life} = \frac{\log_e 2}{\log_e n_2 - \log_e n_1}$$ where $n_1 = 100$ and $n_2 = 100$ - reproductive.

Site	Reproductive	Abort.	New Daughters	Autumn mort.	% survival	Nett	Half-life (years)
H. pilosella							
Acherons	46	3	68	9	69	13	1.1
Ruataniwha	49	2	102	25	75	28	1.0
Wolds 1	79	27	173	30	83	64	0.4
Sawdon	5	3	5	0	100	0	13.5
Glentanner	34	1	53	1	98	18	1.7
H. praealtum							
Acherons	48	6	51	26	48	-23	1.1
Ruataniwha	83	10	159	44	63	32	0.4
Wolds 1	96	32	291	68	77	127	0.2
Sawdon	-	-	-	-	-	-	-
Glentanner	91	4	167	10	94	66	0.3

H. praealtum than *H. pilosella* and this difference increased from 4 to 44% with increasing moisture stress of the sites (Table 3.8).

Annual turnover and population half-life.

From the 100 marked plants per species at each site it was possible to estimate the annual turnover (Table 3.8). The estimated change based only on vegetative reproduction contributions indicates that both species were increasing except *H. praealtum* at the Acherons where a decline occurred.

The half-life of the population was calculated from the equation for exponential decay:

$$t_{\frac{1}{2}} = \frac{t \log_e 2}{\log_e n_2 - \log_e n_1}$$

where $t_{\frac{1}{2}}$ = half-life in years

t = time in years ($t_{n_2} - t_{n_1}$); 1 year was used.

n_1 = number of plants initially present (Spring 1978)

n_2 = number of plants still present excluding recruits (Autumn 1979).

However, since mortality was entirely restricted to reproductive plants of the starting (n_1) population, n_2 can be derived as the product of : n_1 x (number of reproductive plants ÷ 100). This procedure was used to calculate the half-life of sections of colonies of *H. pilosella* at the Wolds 2 site (Table 3.9).

H. praealtum populations had shorter half-lives at all sites except the Acherons site. *H. pilosella* populations

Table 3.9 Zonal variation of reproductive characteristics within *H. pilosella* colonies at Wolds 2 site.

Character	Unit	Zone		t test
		Inner	Outer	
Plant density	(No.dm^{-2})	25.1 ± 3.7	16.9 ± 3.2	9.2***
Reproductive frequency	(%)	1.8	37.9	
	(arcsin %)	7.7 ± 8.3	37.9 ± 5.4	16.7***
Seed production	(No. plant^{-1})	53 ± 8	74 ± 13	9.7***
Total stolon length	(cm)	0.1	14.4	
	(log(cm+1))	0.035 ± .15	1.19 ± 0.49	19.5***
Half-life	(years)	9.0	1.5	

Table 3.10 Means and ANOVA for effect of simulated grazing on stolon production at the Wolds 1 site.

Character	*H. pilosella*		*H. praealtum*	
	Cut	Uncut	Cut	Uncut
Stolon density (No.dm^{-2})	63a	51b	41c	35c
Total stolon length (cm dm^{-2})	1085a	515b	199c	171c

ANOVA		Density		Length	
SV	df	MS	F	MS	F
Species	1	8548	33.5***	9455	133.5***
Grazing	1	2058	8.1**	2230	31.5***
S x G		240	0.9 ns	1840	26.0***
Error		255		71	

at the Sawdon site and in the centre of large (i.e. old) colonies at the Wolds 2 site, were predicted to have a low turnover.

Zonal variation within *H. pilosella* colonies.

The zonal variation of plants within *H. pilosella* colonies (Table 3.7) shows that the marginal plants are much more reproductive than central plants. This difference is related to density as crowded plants virtually ceased to reproduce. These results from within *H. pilosella* patches in the Wolds 2 site where *H. pilosella* only averaged 40% of ground cover compared with the similar low reproduction and replacement by this species at Sawdon where it had become 80% of the vegetation in area and locally pure in many places. The short stolon length in the inner zone is due to the formation of stolon primordia within basal leaf axils but no further development in a high proportion (95%) of the reproductive population.

Effect of simulated grazing

The two hawkweeds responded differently to simulated grazing of the inflorescences (Table 3.10). Although *H. praealtum* was almost unaffected, *H. pilosella* increased the number and doubled the length of stolons formed.

3.5 DISCUSSION

The high country is a difficult environment for establishment from seed. Frost heave on bare sites causes root damage leading to low survival (Gradwell 1955, Simpson and Moore 1955, Scott and Wallace 1978).

H. pilosella and *H. praealtum* relied almost exclusively on vegetative reproduction for population maintenance (Table 3.6). While there can be no question that pioneer plants, even at the microsite level, arose from seed,

vegetative reproduction was the tactic used to increase the extent of their existing populations (Tables 3.7 and 3.8). Although vegetative reproduction had a large parental investment per propagule compared with seed (Fig. 3.5), establishment success for both species was high (Table 3.8).

If vegetative reproduction is a key tactic of the perennial strategy under adverse conditions, then superiority of this tactic in terms of number of offspring and distance of spread from the parent should be advantageous. Conversely, relatively higher seed production would accrue better colonisation potential for locating suitable sites beyond the range of immediate clonal spread.

The decline in seed production in *H. pilosella* with extensive patch development (Table 3.9) therefore severely limits the distant colonising potential of this species compared with *H. praealtum*. Under favourable conditions, high seed production may also make some additional contribution to population maintenance (Table 3.8). Thus, the tactical variations found in the regenerative strategies of *H. pilosella*, *H. praealtum* and *H. lachenalii* (Fig. 3.4), may partially define their habitat preferences.

H. pilosella produced less seed but more daughters which established further from the parent compared to *H. praealtum* (Table 3.7). Furthermore, *H. praealtum* was inferior in autumn survivorship of daughters. This difference progressively increased from 4% to 44% in favour of *H. pilosella* going from the low stress site (Glentanner) to the high stress site (Acherons)(Table 3.8). The net population addition (Table 3.8) adjusted for plant density (Appendix B), shows that both species gained equal amounts

of new ground through vegetative reproduction at the two lowest stress sites (Glentanner and Wolds 1). However, *H. pilosella* advanced by 50% more than *H. praealtum* at the next higher stress site (Ruataniwha). Although *H. pilosella* also increased in area at the highest stress site, the number of surviving *H. praealtum* daughters failed to balance spring plant loss through reproduction, causing a retreat of this species.

Grazing also modified regenerative potential. Sheep grazing briefly in the study area at the time of inflorescence formation removed inflorescences and thereby eliminated seed production.

A secondary effect of inflorescence removal was the improvement of the already superior vegetative reproduction, especially spread, of *H. pilosella* but produced only minimal changes in this respect to *H. praealtum* (Table 3.10).

The production of dry matter by *H. pilosella* was very low compared to *H. praealtum* (Table 3.5) or especially the common pasture grasses and legumes (Scott 1979). These figures do not indicate the difference in herbage availability or palatability. *H. pilosella* had a flat habit compared to the erect form of *H. praealtum*. The latter species also tended to produce most leaf growth in spring and autumn flushes interspersed by inflorescence formation. Consequently *H. praealtum* was physically more available, when present, to sheep and because the foliage was of more recent origin, it was probably more palatable as well. The Ribbonwood Study (Scott and Maunsell 1974, Hughes 1975) in North Otago shows that *H. praealtum* is a favoured species (i.e. diet abundance

cp. field abundance) in developed and undeveloped grassland. Over all months, *H. praealtum* was the 6th and 4th most popular species in the developed and undeveloped blocks respectively compared with *H. pilosella* at 20th and 17th positions. The nutritive value (protein, P, K, Mg, Fe and Zn) of *H. praealtum* was generally the same as *Hypochoeris radicata* (Grace and Scott 1974), which was the next, or immediate to next, higher species in the dietary order (Hughes 1975). Since *Hypochoeris radicata* is recognised as being of benefit in undeveloped grasslands (Cockayne 1967), a similar case can be made for *H. praealtum*. The moderate dry matter production of *H. praealtum* in moister parts of the Mackenzie Country ranged from 0.27 - 1.35 tonne DM ha^{-1} $annum^{-1}$ with unimproved soil fertility, a level comparable with other resident species.

H. Pilosella populations are probably more stable than *H. praealtum* populations based on the differences in potential half-life (Tables 3.8 and 3.9). Turnover in the populations studied was entirely confined to death following reproduction. Therefore the higher reproductive frequency of *H. praealtum* means an increased risk of population decline if establishment failure should happen to parental replacements, as occurred at the Acherons site.

Plant performance (adult stage) in terms of growth, production and reproduction was used to define the response of the two hawkweeds to broad environmental variation. While both species did best at the intermediate sites with moderately fertile, deeper soils under 600-675 mm annual precipitation, distinct habitat preferences emerged. The general

performance and root-shoot data indicated that *H. praealtum* was better in the moist sector and responded to increasing moisture stress by allocating proportionately more biomass to the root system. However, at the driest site, this response was not sufficient judging by the fall in total performance and subsequent population decline caused by low establishment of daughters. These effects were probably accentuated by the dry January period. *H. pilosella* had a very uniform growth response to varied conditions (Fig. 3.6) and matched or exceeded *H. praealtum* in various respects at the drier site. This wide edaphic-climatic tolerance is probably the reason for the abundance of *H. pilosella* throughout much of its present geographic range.

CHAPTER 4

ECOPHYSIOLOGY: GERMINATION, SEED MORPHOLOGY, SOIL FERTILITY, AND HERBICIDE EXPERIMENTS

4.1 INTRODUCTION

Chapter 3 described some of the contrasts in growth and reproductive characteristics of *H. pilosella* and *H. praealtum* in the environments in which they occurred. To understand how these sites were colonised, and why the patterns differ between sites, it is necessary to understand some of the ecophysiological characteristics of the species. Examination of the various life stages is necessary however for as Grime (1979) has pointed out, adaptations may vary at different life stages because the environment experienced by the species may also vary at the different stages.

The experiments described in this chapter examine the performance of *H. pilosella* and *H. praealtum* at different stages in their life history, particularly the germination and early seedling growth, in relation to some environmental (physical and soil) and managemental (fertilisers and herbicides) factors.

Initial field observations suggested that *H. praealtum* tended to establish on recently bared ground and *H. pilosella* on open vegetated sites. In Britain, Watt (1962) found that *H. pilosella* did not establish new seedlings over a period of several years even though there was a regular input of seed. The exception occurred in years of higher than average spring rainfall, suggesting critical germination

requirements for moisture in this species. Thompson (1973) claims that relatively small differences in germination responses may cause much of the delimitation of range and habitat preferences of a species as the timing of germination largely predetermines the survival of a seedling to maturity.

Although *H. pilosella* is characteristic of nitrogen deficient soils in Europe (Ellenberg 1974), Canadian experience indicates that it is responsive to nitrogen and phosphorus fertilisation (Meylaender 1968). The Mackenzie country high country yellow-brown earths and similar soils in other districts are deficient in nitrogen, phosphorus, sulphur and molybdenum (N.Z. Soil Bureau 1968). Correction of the deficiencies is essential to realise the production inherent in the introduced pasture species. The effect of increases of these nutrients on resident hawkweed communities is not known. Initial observations of *H. pilosella* and *H. praealtum* at DSIR plant testing trials, where molybdenum and sulphur fortified superphosphate fertilisers or nitrogen fertilisers had been used, were that while both species responded in terms of yield, *H. pilosella* became particularly expansive through vegetative reproduction.

Soil fertility may be modified by plants themselves. It has been shown that some plants were able to inhibit nitrification *in vitro* (Moore and Waid 1971, Neal 1969). Neal (loc. cit.) suggested that this control, which was largely confined to invader or weed species of heavily grazed grasslands could be a response to conserve nitrogen. If pasture grasses have greater nitrogen requirements than *H. pilosella*, a depression of the level of available nitrogen in the rhizosphere could enhance the competitive advantage

of this species.

4.2 EXPERIMENTAL

Germination response

Seed was collected from *H. piloselLa* and *H. praealtum* populations on the Wolds 2 site in January 1975, mixed and stored in paper envelopes in the laboratory prior to use. An immediate viability test was performed at 20^{o} using the procedures given below.

The temperature response was determined on three month old laboratory stored seed at 2^{o}, 17^{o}, 22^{o}, 27^{o} and 32^{o} with a thermobar in a growth room under a 16 h daylength photoperiod provided by daylight fluorescent plus some incandescent light banks (180 microeinsteins m^{-2} sec^{-1}). Six replicates of 50 seeds each were germinated on two layers of Whatman #2 filter paper moistened with distilled water, in 9 cm petri dishes. Germinated seeds were counted and removed daily until the cumulative germination reached a plateau. The time to 50% germination was interpolated from cumulative germination curves.

The presence of a light requirement was determined under conditions of light and total darkness at 20^{o} for 22 days with otherwise the same lighting and germination procedures given above, except that three replicates per treatment were used.

The influence of moisture availability on germination of both hawkweeds compared with a range of pasture species was evaluated using osmotic solutions. The test solution must satisfy three criteria according to Slavik (1974): it

must not be harmful to living cells; the cytoplasmic membranes should be practically impermeable to the solute; and the solute should not be metabolised. Sucrose, mannitol and polyethylene glycol are the most commonly used osmotica but none completely fulfills all three requirements. Sucrose is a small molecule and consequently permeable to cells. While polyethylene glycol has the lowest permeability, it has serious toxic effects which users (e.g., Mott 1974, Lagerwerff *et al.* 1961) have failed to acknowledge (Lawlor 1970).

Solutions of mannitol were used at 0, -1, -3, -7, -11, and -15 atmospheres with solutions renewed weekly. Four replicates of 25 seeds per species per treatment were maintained at 20^{o} with a 16 h daylength photoperiod (180 microeinsteins m^{-2} sec^{-1}).

Field observations were made at the Mackenzie country during 1974-6 and 1978-9 to describe the pattern of germination and establishment.

Seedling biology

Seed weight of both species was determined from three replicates of 1 000 seeds. Post germination dependence on endospermic resources was evaluated from one hundred dish germinated seeds of each species transferred to grow on germination paper with about 20 ml distilled water in 9 cm petri dishes (25 seedlings per dish) at 20^{o} under light conditions of the growth room used in the germination experiment. After three weeks, root length was measured with calipers, shoots air dried and weighed and the number

of chlorotic seedlings counted. Chlorosis was taken as yellowing of more than 25% of the leaves and cotyledons.

Seedling morphological light response

Dish germinated cotyledonous seedlings (about 7 days post germination) were planted singly in 250 cm^3 of unamended soil from the Wolds 1 site in 7 x 7 cm pots in a 20^{o} growth room used in the previous experiments.

Different gradients of light were produced by the presence of vertical tubes of two types made from inverted pots with the ends removed. For a maximum gradient, the inside walls were painted matt black. Unpainted tubes gave a lesser gradient. The pots were arranged so that the main light bank (180 microeinsteins m^{-2} sec^{-1}) was about 45^{o} to one side. The relative light intensities measured photoelectrically at the height of the seedlings were: no tube = 100, white tube = 40 and black tube = 8. Each treatment had eight replicates. Seedling height and leaf number were measured and counted after 7 weeks and mortality after 16 weeks.

Adult plant shade response

The effect of shading on habit and morphology of adult plants was studied in the Botany Department shadehouse. Parts of clones of both hawkweeds from Wolds 1 site were cut out with soil to fit shallow boxes (1 x 0.5 x 0.15 m). Each box contained about 600-1 000 plants. One box of each species was placed in uncovered and lath covered shadehouses (10% light transmission). The size (7 x 5 x 2.5 m) of these

structures was sufficient to ensure good ventilation preventing noticeable air temperature differences. A basal leaf from 40 plants chosen at random was measured using calipers for each treatment after one growth season (August 1976 - May 1977).

Nitrogen and phosporus levels under *H. pilosella* colonies

At the Wolds 2 site 12 cores of 10 cm diameter x 7.5 cm deep were taken from a dense *H. pilosella* patch (about 30 plants dm^{-2}) and from adjacent vegetation (mainly *Agrostis tenuis*, *Anthoxanthum odoratum* with about one *H. pilosella* plant dm^{-2}). Samples were kept at field temperatures for 12 h before reaching the laboratory where they were held at 2^{o} for about 48 h prior to analysis. Samples were sieved to remove root material and the soil moisture content determined from a 10 g sample of each core as the loss of weight after drying for 24 h at 105^{o}.

Available nitrogen was determined by the incubation method of Bremner (1965 p.1330-41). This method is based on the estimation of mineral nitrogen produced when a soil sample is incubated under standard aerated conditions which promote mineralisation of nitrogen from organic forms in the soil. Incubation methods are generally accepted as giving the most satisfactory assessment of potentially available nitrogen for plant growth (*loc. cit.*). A 10 g sample of undried soil which had passed through a 2 mm mesh sieve was mixed with 30 g of acid-washed 45 mesh fine quartz sand and transferred to a flat bottomed incubation flask. Exactly 6 ml of distilled water less the amount estimated

to be present from the moisture determination was added and the sample evenly distributed in a thin layer across the bottom of the flask. A seal to allow gaseous exchange but prevent evaporation was made by securing thin polyethylene film ("Gladwrap") over the top. The flask was incubated in the dark at 20^{o} for 14 days. After incubation, 100 ml of 2N KCl was added and the contents of the flask agitated for 1 h with the top resealed. The contents were allowed to stand for 30 min before removing a sample for analysis.

The amount of ammonium-nitrogen (NH_4-N) and nitrate-nitrogen (NO_3-N) present in the soil before incubation and in an aliquot of KCl soil extract after incubation were determined titrimetrically by the magnesium oxide-Devarda alloy steam distillation procedure (Bremner 1965 p.1195-8) from a 5 g sample and 25 ml aliquot respectively. It was assumed that nitrite-nitrogen (NO_2-N) was extremely short-lived and removed rapidly. If present, it would have been recovered in the NO_3-N distillate. Three replicates from a composite of 4 cores from each vegetation type were analysed and corrected for the original moisture content.

Available phosphorus was extracted from 100 g of field moist soil with 250 ml of 2.5% (v/v) acetic acid and estimated colorimetrically by the molybdenum blue method (Allen *et al.* 1974 p.50, 206-9) using the previous replication and corrections.

Fertiliser pot trials

In a glasshouse pot trial, visually similar sized five-leaf plants (average shoot weight 16 mg) of *H. pilosella*

and *H. praealtum* were planted singly in 9 x 9 cm plastic pots containing 425 cm^3 of 4 mm sieved unamended yellow-brown earth soil collected from the Wolds 1 site. The potted soil was amended two months prior to transplanting with three levels of nitrogen (0, 0.4 and 0.8 g per pot of calcium nitrate (26% N) which is equivalent to 0, 125 and 250 kg ha^{-1} respectively) and two levels of sulphur and molybdenum fortified superphosphate (0 and 0.4 per pot which is equivalent to 0 and 500 kg ha^{-1}) in a balanced factorial design with six replicates. Herbage was harvested after 10 weeks growth in September 1975, dried at 80^{o} for 3 days and weighed. The herbage yields were logarithmically transformed and analysed by a factorial ANOVA (Sokal and Rohlf 1969).

A similar experiment was performed using two levels of nitrogen and phosphorus (0 and 125 kg ha^{-1}, 0 and 500 kg ha^{-1} respectively) with six replicates to examine the effect of soil fertility on the number and total length of stolons per plant in both species at the end of a season of growth (August 1975 - May 1976). Stolon length was transformed logarithmically ($\log_{10}Y + 1$) and data analysed using a factorial ANOVA.

Field herbicide trial

In a trial laid down by Ivon Watkins-Dow Ltd., a range of herbicides (Table 4.10) was evaluated for control of *H. pilosella* in grassland. The trial was at the Sawdon site where about 80% of the vegetation was *H. pilosella*, 5% *Trifolium hybridum* (alsike) and the remainder mainly *Agrostis tenuis* and *Anthoxanthum odoratum*. The herbicides

were applied when *H. pilosella* was flowering using a boom sprayer from 0.7 m during dry weather on 1 December 1978 at 5.30 a.m.

Observations on this trial of plant appearance were made during December and January, a count of *H. pilosella* plants surviving per dm (n = 30 per treatment), and alsike vigour scored (0 = dead shoot to 5 = normal) on 12 February 1979. Further observations on *H. pilosella* regrowth and alsike and grass appearance were made on 6 March 1980.

4.3 RESULTS

Germination in vitro

The storage period of three months had no effect on the germination of either species (Table 4.1a). A well-defined light requirement was found in *H. praealtum* seed. Darkness reduced the germination of *H. pilosella* to a minor degree.

H. pilosella seed germinated most rapidly at 22^{o} which was 5^{o} lower than the optimum for *H. praealtum*. *H. praealtum* germinated well over a 17-32^{o} range exceeding 50% germination at all temperatures. *H. pilosella* was restricted by the higher temperature (32^{o}) (Fig. 4.1, table 4.1 b,c). At 2^{o}, only *H. praealtum* germinated after 21 days. *H. pilosella* began germinating after this time and reached 13 ± 7% compared with 16 ± 9% for *H. praealtum* at 80 days. Fungal growth appearing after about 10-15 days precluded long-term high temperature experiments. Widespread attack occurred in the fourth week.

H. pilosella was more restricted by moisture stress applied by an osmoticum than *H. praealtum*. The tolerance

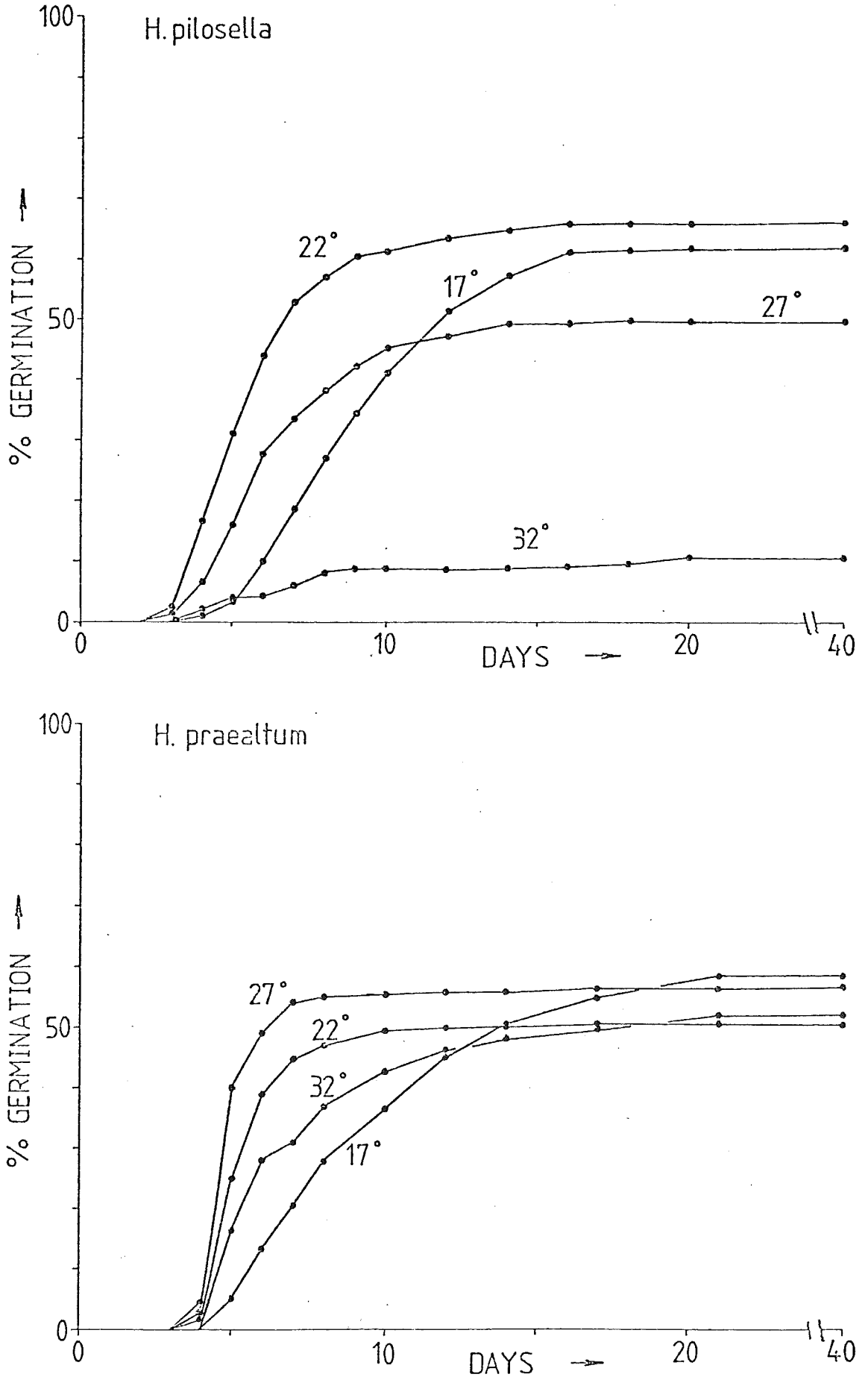


Figure 4.1 Cumulative germination of *H. pilosella* and *H. praealtum in vitro* at 17°, 22°, 27° and 32°.

Table 4.1 Effect of storage, light, temperature and osmotic stress on the germination of *H. pilosella* and *H. praealtum*. Values in brackets are either a t or t′ test.

Treatment	*H. pilosella* mean ± se		*H. praealtum* mean ± se	
(a) Storage and light response (% germination)				
Fresh seed	67 ± 7	(0.7 ns)	54 ± 7	(0.3 ns′)
3 m - light	64 ± 7		55 ± 5	
- dark	49 ± 7	(3.7***)	12 ± 2	(19.6***′)
(b) Temperature response (% germination)				
2°	0		1 ± 1	-
17°	62 ± 8		58 ± 6	(1.0 ns′)
22°	66 ± 12		50 ± 8	(2.7*′)
27°	50 ± 2		56 ± 8	(1.8 ns′)
32°	11 ± 6		52 ± 12	(7.5***′)
(c) Temperature response (Days to 50%)				
2°	-		-	
17°	12.8		14.0	
22°	6.7		14.0	
27°	18.0		6.2	
32°	-		18.5	
(d) Osmotic stress (Germination % of control)				
1 bars	85 ± 5		97 ± 5	(3.4*)
3 "	62 ± 11		99 ± 2	(6.6**′)
7 "	20 ± 12		62 ± 12	(5.0**)
11 "	0		12 ± 8	
15 "	0		0	

difference was about 4 bars in the -3 to -11 bars range (Table 4.1d). Although *H. pilosella* was inferior under moisture stress compared to the four pasture species used, *H. praealtum* was similar to *Trifolium hybridum*, *T. repens* and *D. glomerata* (Fig. 4.2).

Field germination and establishment

Germination was rare in both species, particularly compared with other resident species. *Crepis capillaris*, the resident species most closely related to *Hieracium*, while in low abundance, had noticeably more seed germinate than either *H. pilosella* or *H. praealtum*. There was a low incidence of *Hieracium* germination about April-May and August-October in 1974-6 and 1978-9 (no observation at other dates). Climate records for the Lake Tekapo region show that during these months favourable surface moisture levels occurred but temperatures were very low (Table 4.2). Distinct flushes of germination occurred near the end of moist intervals (about 5-8 days duration) at the warmest period in January and February 1979.

Virtually all *Hieracium* seedlings were short-lived. The few exceptions were established from the short, summer germination episodes. These seedlings grew quickly and became adult sized in about 8-10 weeks. One *H. pilosella* and three *H. praealtum* seedlings survived into mid April 1979 in a 25 m^2 plot at the Ruataniwha site.

Seedling biology

The seed weight of *H. praealtum* was less than that of *H. pilosella*, indicating lower seed reserves for initial

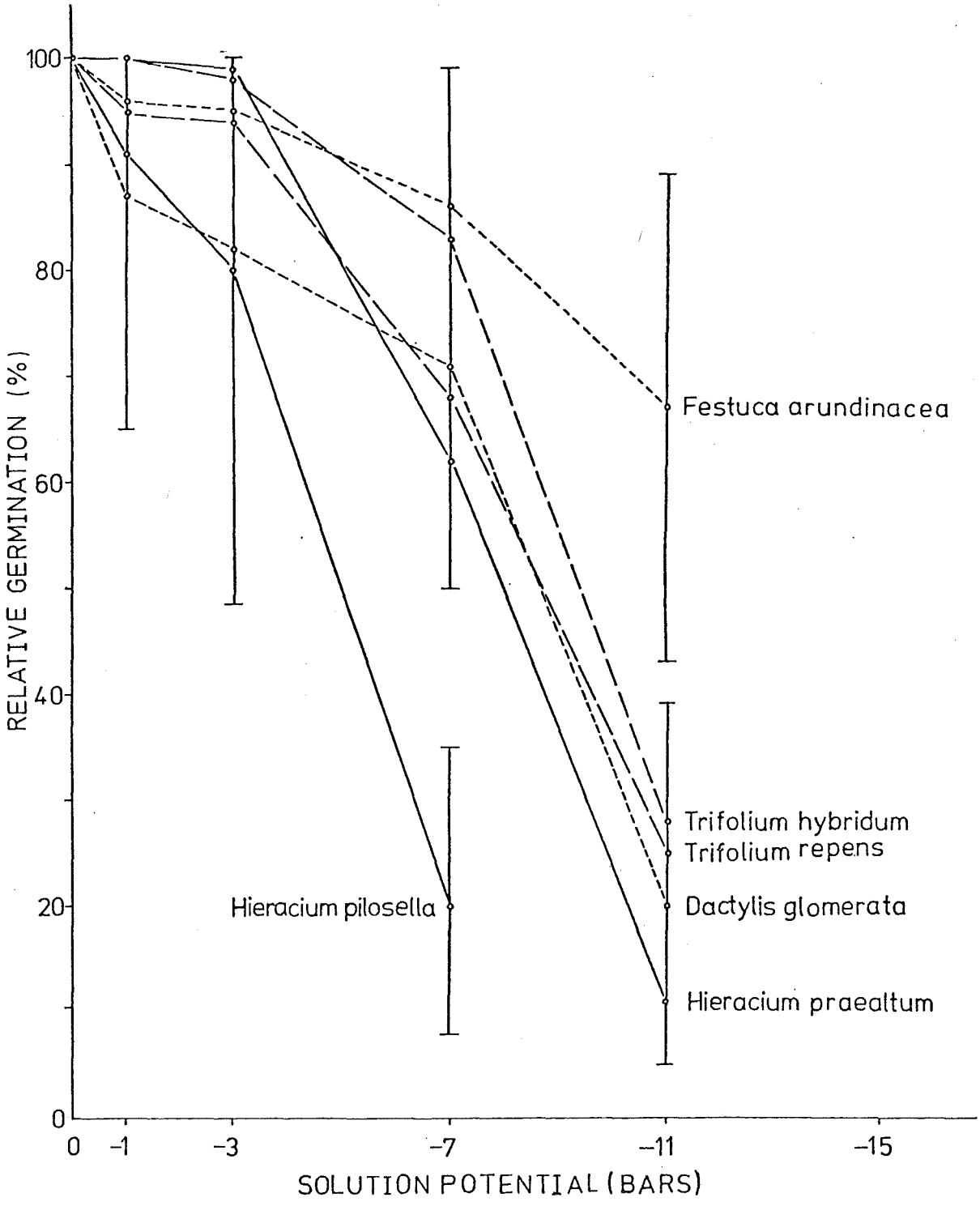


Figure 4.2 The effect of osmotic stress on the germination of *H. pilosella*, *H. praealtum* and four pasture species. The 95% confidence interval is indicated by vertical lines.

TABLE 4.2 Long term temperature and soil moisture records from the Lake Tekapo district (N.Z. Meteorological Service)

Period	Degree-days[1] (above 5° C)	Moisture[2] Deficit (mm)	Runoff[2] (mm)
January	260	38	-
February	238	38	3
March	196	33	
April	114	13	5
May	35	3	13
June	10	-	23
July	4	-	38
August	9	-	33
September	38	-	20
October	100	-	13
November	139	8	8
December	209	28	3
Year	1354		

1 Mt. John (1 027 m) 1941-70

2 Lake Tekapo (683 m) 1925-70

growth until the seedling became autotrophic (Table 4.3). This difference was corroborated by the greater incidence of nutrient deficiency symptoms (chlorotic appearance) which occurred among *H. praealtum* seedlings. More shoot growth and less root growth was found in *H. praealtum* than in *H. pilosella* at 3 weeks.

H. pilosella showed a marked reduction in leaf number, and only a small increase in seedling height compared to *H. praealtum* in relation to the light gradient (Table 4.4). The growth of *H. pilosella* in response to the gradient came from hypocotyl growth whereas *H. praealtum* elongated more in the petiole region. As a consequence, seedlings of the former species were physically frail. After 16 weeks, there was complete mortality of the seedlings in the strongest gradient.

Adult plant shade response

H. praealtum was the longer-leaved species (Table 4.5). Under shade conditions, it was also able to respond more than *H. pilosella* both in absolute and relative amounts.

Nitrogen and phosphorus levels under *H. pillosella* colonies

No difference in available nitrogen was found between the different vegetation types (Table 4.6). Available phosphorus was appreciably lower under near pure *H. pilosella* stands. These regions also had the lowest reproductive frequency, shortest stolon lengths and lowest seed production compared with the isolated marginal plants expanding into

TABLE 4.3 Seed and seedling characteristics of *H. pilosella* and *H. praealtum*

Character	*H. pilosella*	*H. praealtum*	t test
Seed weight (mg 1 000^{-1})	175 ± 8	141 ± 8	5.2**
21 day root length (mm)	56 ± 11	46 ± 9	3.1**
21 day shoot weight (mg)	21 ± 5	37 ± 7	8.3***
21 day chlorosis (%)	23 ± 42	67 ± 47	7.0***

TABLE 4.4 Mean seedling height (mm), number of leaves, and ANOVA of *H. pilosella* and *H. praealtum* at 8 weeks under different light gradients

	Seedling height (mm)	
Light gradient	*H. pilosella*	*H. praealtum*
None	8.8 ± 1.8 c	12.3 ± 3.0 c
Intermediate	17.1 ± 4.2 b	16.6 ± 3.5 b
Maximum	11.3 ± 4.0 c	21.5 ± 3.3 a

	Number of leaves	
Light gradient	*H. pilosella*	*H. praealtum*
None	5.8 ± 1.2 a	4.5 ± 0.9 b
Intermediate	4.6 ± 1.1 b	4.1 ± 0.6 b
Maximum	0.8 ± 0.7 d	2.3 ± 0.5 c

ANOVA		Seedling height		Number of leaves	
SV	df	MS	F	MS	F
Species	1	234.08	20.5***	0.08	0.1 ns
Gradients	2	201.08	17.6***	58.58	78.7***
S x G	2	118.08	10.3***	8.08	10.9***
Error	42	11.41		0.74	

TABLE 4.5 Leaf length (mm) of adult *H. pilosella* and *H. praealtum* plants under open and shade (10%) conditions.

Light	*H. pilosella*	*H. praealtum*	t' test
Open	27 ± 4	46 ± 10	11.2***
Shade	50 ± 11	137 ± 24	20.8***
Shade:Open	1.9 ± 0.5	3.0 ± 0.8	7.4***

TABLE 4.6 Available soil nitrogen and phosphorus beneath a low and high density area of *H. pilosella* at Wolds 2 site

Dominant Vegetation	Available soil N (ug N g^{-1} soil)		Available soil P (mg 100 g^{-1} soil)
	NH_4	NO_3	
H. pilosella	0	43 ± 3	1.2 ± 0.4
Festuca novae-zelandiae and *Agrostis tenuis*	0	43 ± 3	2.9 ± 0.4
			t = 5.2**

the fescue tussock-browntop areas (Table 3.9).

Fertiliser response

The pot fertiliser experiment showed there was a significant difference between the two species in their interaction with nitrogen and superphosphate fertiliser (Table 4.7). Both species had the greatest growth at the intermediate nitrogen level and the higher superphosphate level. *H. pilosella* was more fertiliser responsive than *H. praealtum* (x 18 cf. x 4 increase between lowest and highest treatment).

Species × nitrogen interactions were found for stolon number (Table 4.8). *H. praealtum* showed no response to raised nitrogen. *H. pilosella* produced fewer stolons under the basal nitrogen level and more under the raised level than *H. praealtum*. Species × superphosphate interactions were present for total stolon length (Table 4.9). *H. pilosella* formed longer stolons than *H. praealtum*, which did not respond under superphosphate amendment.

Herbicide response

2,4-D ester + D290 at 1 000+400 g ha^{-1} and 750+300 g ha^{-1} gave the best control of *H. pilosella* (Table 4.10). Although this application caused damage to the resident clover (alsike) in the immediate post spray period, by March 1979 this clover was healthy in all plots. Regrowth by *H. pilosella* was very slight (about 1 plant m^2) in the best controlled plot but almost indistinguishable from unsprayed areas in the least effective application plots.

TABLE 4.7 Mean shoot yield and ANOVA under different soil fertility levels on a low organic matter YBE soil N0 = nil, N1 = 125 and N2 = 250 kg ha^{-1} calcium nitrate, P0 = nil, and P1 = 500 kg ha^{-1} S Mo fortified superphosphate. Mean log_{10} (weight mg) with arithmetic mean in brackets.

Treatment	*H. pilosella*		*H. praealtum*	
	P_0	P_1	P_0	P_1
N0	1.38 (24) g	1.35 (22) g	1.70 (50) f	1.71 (51) f
N1	1.94 (87) def	2.82 (660) a	2.18 (151) cd	2.52 (331) bc
N2	1.90 (79) ef	2.63 (427) ab	2.09 (123) cde	2.33 (214) c

ANOVA

SV	df	MS	F
Species	1	0.130	3.1***
Nitrogen	2	4.835	111.2***
Phosphorus	1	2.351	54.1***
S x N	2	0.288	6.6**
S x P	1	0.493	11.3**
N x P	2	0.646	14.9***
S x N x P	2	0.152	3.5*
Error	60	0.043	

TABLE 4.8 Treatment means and ANOVA of stolon length per plant under different soil fertility levels.

N0 = nil, and N1 = 125 kg ha^{-1} calcium nitrate. Mean log_{10} (length cm) with arithmetic mean in brackets

Treatment	*H. pilosella*	*H. praealtum*
N0	0.05 (1.1) c	0.28 (1.9) b
N1	0.51 (3.2) a	0.31 (2.0) b

ANOVA

SV	df	MS	F
Species	1	0.0017	0.1 ns
Nitrogen	1	0.3525	14.7*
Phosphorus	1	0.1069	4.5 ns
S x N	1	0.2723	11.4**
S x P	1	0.0235	1.0 ns
N x P	1	0.02345	1.0 ns
S x N x P	1	0.0016	.3 ns
Error	16	0.0240	

TABLE 4.9 Treatment means and ANOVA of number of stolons formed under different soil fertility levels. P0 = nil, and P1 = 500 kg ha^{-1} S Mo fortified superphosphate mean log_{10} (number) with arithmetic mean in brackets (p = 0.05)

Treatment	*H. pilosella*	*H. praealtum*
P0	0.13 (1.3) b	0.29 (1.9) b
P1	1.34 (22.4) a	0.35 (2.2) b

ANOVA

SV	df	MS	F
Species	1	1.062	24.8***
Nitrogen	1	0.566	13.2**
Phosphorus	1	2.466	57.6***
S x N	1	0.136	3.2 ns
S x P	1	2.003	46.8***
N x P	1	0.102	2.4 ns
S x N x P	1	0.027	0.6 ns
Error	16	0.043	

TABLE 4.10 Herbicide response of *H. pilosella* at Sawdon site

Herbicide Treatment	Rate Active Ingredient (g ha^{-1})	Hieracium Survival (No dm^{-2})	Alsike Vigour (5=high, 1=low)
2,4-D ester	1440	3.3 e	5
2,4-D + pichloram	800 + 200	5.0 d	3
2,4-D amine + D290	800 + 300	19.1 b	3
" " "	1200 + 450	7.8 c	1
2,4-D ester + D290	750 + 300	0.1 g	2
" " "	1000 + 400	0.0 g	1
" " "	1000 + 58	4.0 de	4
" " "	1500 + 87	1.7 f	3
Control		30.2 a	5

4.4 DISCUSSION

Seed germination is influenced by a number of external factors, usually moisture, temperature and, for certain species, light. These factors vary widely in the tussock grassland habitat. Temporal variation occurs during daily and seasonal climatic changes. Spatial variation (habitat heterogeneity) is produced by the size and extent of the tussocks and different types of ground cover in the inter-tussock areas (Scott 1962). In the dry-hygrous zone where the hawkweed populations predominantly exist, habitat variation across distances of only a few centimetres frequently determines species occurrence from seed (Scott 1961, 1978). Bare soil was the least favourable place for seed to germinate (Scott *loc. cit.*).

The relatively greater success of *H. praealtum* compared to *H. pilosella* on bare sites was consistent with their germination ecophysiology. The absence of a light requirement (Table 4.1a) in seed of *H. pilosella* would permit germination of seed among litter or when buried. More favourable moisture and temperature conditions in these locations (Dowling *et al.* 1976) than on the surface would tend to restrict germination of *H. pilosella* seed to such places. The higher temperature optimum and extreme, and the greater moisture stress tolerance of *H. praealtum* seed would allow it to penetrate further into the bare habitat than *H. pilosella*. However the light induction requirement of most *H. praealtum* seed would limit its germination capacity in vegetation.

H. pilosella and *H. praealtum* were rapid germinaters

in vitro at warm temperatures (Fig. 4.1). This has also been reported for other hawkweeds (Grime 1979, Panebianco and Willemsen 1976, Stergios 1976, Thomas and Dale 1976, Vander Kloet 1978). Germination was possible from newly formed seed immediately, without after-ripening, providing suitable conditions occurred. Normally, temperatures favouring rapid germination occurred when soil moisture conditions were least favourable. The very small amount of germination noted during the April-May and August-October periods, cf. wet summer periods, was probably a result of the low temperatures, since moisture availability at the soil surface was favourable. The prolonged germination period necessitated by the low temperature would have greatly increased the loss of viable seed to fungal pathogens. The germination flushes seen after brief wet intervals during very warm weather in January and February suggest that except when favourable temperatures coincided with adequate moisture (atypical), the germination of both species would be restricted to autumn and spring. Since persistent seed reserves are not incorporated into the soil by hawkweeks (Grime 1979, Panebianco and Willemsen 1976, Thomas and Dale 1976, Pugsley 1948), higher levels of germination can only occur after seed dispersal around December.

Virtually all seedlings produced by each species were ephemeral and never passed the cotyledon stage. On bare soil, frost heave effects (Gradwell 1955, Simpson and Moore 1955) and freezing damage (Vander Kloet 1978) were the likely reasons for most mortality. In vegetated sites, seedlings which did not succumb to freezing were suppressed

under new growth of taller plants. The exceptional seedlings were established from summer germination and quickly grew to a size which appeared both competitive and winter hardy. Even then however the chances of a seed becoming a seedling of this type was estimated to be about 1 in 230 000 for both species in 1978-9 at the Ruataniwha site.

Grime (1979) considers plants can be classified into a number of basic types based on their strategy of adaptation to stress and disturbance in the habitat (Table 4.11). By this classification *H. praealtum* and *H. pilosella* were R-S and C-S-R strategists respectively. *H. praealtum* produced a large number of light seeds with low levels of reserves. These features are characteristic pioneering tactics to locate elusive habitats (Cavers and Harper 1966, 1967, Grime 1965, Salisbury 1942). While most grassland species, even of open vegetation, (e.g., *H. pilosella*) have little or no light requirement, most bare ground colonisers (R-strategists) do (Grime and Jarvis 1975). Relatively greater seedling shoot to root development and shoot response to shading is adaptive where rapid capture of leaf space is possible and is not restricted by root competition. Within the more stable habitat which *H. pilosella* colonises, root competition is present at the outset of seedling appearance and probably intense due to the potentially low production by the community (Grime 1979). The larger seed reserves and more root development in *H. pilosella* are favourable adaptations for this habitat.

In the ruderal habitat which *H. praealtum* favoured, conditions during germination and establishment (disturbed

TABLE 4.11 Alternative plant strategies (after Grime 1979 p.7)

Strategy Type	Stress Tolerance	Disturbance Tolerance
Competitor (C)	Low	Low
Stress tolerator (S)	High	Low
Ruderal (R)	Low	High
Not viable	High	High
C-S-R	Moderate	Moderate

soil, no competition for soil or leaf space) change as colonisation proceeds. In contrast, *H. pilosella* occupied a relatively constant habitat at each life stage. The superior shoot response of *H. praealtum*, particularly to shading, at the seedling stage also continued in the adult plants, an appropriate response for existence in an ungrazed herbaceous community. The limited response to shading, and the short leaved, flat habit of *H. pilosella* were adaptive responses and morphology for grazed habitats.

Since *H. praealtum* had primary colonising abilities it was likely to have benefitted by occasional, extensive site disturbance compared with species which appear after colonisers enter the site, and preferred stable, more developed conditions. *H. pilosella* is more suited to essentially stable habitats which received regular low intensity foliar damage which would restrict competitors with the potential for overgrowth. Seed is much less important compared to vegetative reproduction under these conditions once a few localised pioneers have entered the habitat, favouring *H. pilosella* cf. *H. praealtum*.

Based on the soil fertility responses, *H. praealtum* is a species of low to moderate fertility soils. *H. pilosella* preferred higher soil fertility. Unlike *H. praealtum*, vegetative reproduction of *H. pilosella* was strongly influenced by fertilisers. The number of stolons formed and the potential number of vegetative offspring increased with nitrogen amendment. Petersen (1979) also found that increased nitrogen availability produced more vegetative propagation per plant in *H. florentinum*. The

length of stolons and hence the expansive ability of *H. pilosella* was greatly increased by superphosphate. The sensitivity of *H. pilosella* to nutrient levels in the soil may provide some explanation of the zonal variation of size and reproduction of this species when it formed colonies. It is reasonable to expect the amount of nutrients available per plant would be lower in the dense inner zone of the colony than at the open marginal zone. This difference alone appeared sufficient to control plant vigour and reproduction since shallow rabbit scratchings which removed plants usually caused vigorous growth and better reproduction of the immediately adjacent plants. Since *H. pilosella* sends stolons out radially in the development of a colony, it is possible that some export of nutrients from the older central zone may accentuate this effect. Although available soil nitrogen was unaffected by *H. pilosella*, available phosphorus was appreciably lower under *H. pilosella* in the inner zone than the outer region. The absence of marked fertility responses and zonation of *H. praealtum* colonies are consistent with these hypotheses.

The pattern of animal droppings and urine may be important in redistributing nutrients within a grassland since phosphorus is returned to the pasture as droppings and nitrogen in urine (Duffy *et al.* 1974). Rabbits show a definite preference for open, short vegetation (Howard 1958). Even during the mid 1970s when rabbit numbers were low compared with earlier periods, rabbit droppings on *H. pilosella* and other mat-forming species, were more common than on taller species.

This differential return of nutrients may be greater at the moment when distinct mosaics of vegetation of different height occur than thirty or so years earlier when rabbits were more common and vegetation was uniformly depleted.

The herbicide Dowco 290 with 2,4-D esters gave better control compared to previously recommended herbicides (Matthews 1975) although *T. hybridum* and the two main grasses, *Anthoxanthum odoratum* and *Agrostis tenuis* were severely affected during the 2-3 months post spraying. However, after one year these species were completely recovered along with a small but significant amount of *H. pilosella*. It is imperative to autumn sow immediately in order that establishment of new pasture prevents a reoccurrence of *H. pilosella* dominance from these survivors. For comparison however, a good strike of pasture species and topdressing brought *H. pilosella* under control within two years and to a low incidence within three years at the Sawdon site (see Chapter 6). The additional cost of herbicide needs to be compared with the cost due to production lost by the amount of *H. pilosella* present in the initial period of the non-chemical approach. The cost effectiveness of herbicides is better in the potentially productive regions where straight oversowing and topdressing will also perform well.

CHAPTER 5

ALLELOPATHIC AND COMPETITION EFFECTS OF *HIERACIUM PILOSELLA* AND *H. PRAEALTUM*

5.1 INTRODUCTION

The processes of one plant which are deleterious to another plant of the same or different species at any life-history stage are termed interference (Muller 1969). Two categories of interference phenomena are usually recognised. Allelopathy is the name given by Molisch (1937) to biochemical interactions between plants of all types while competition refers to situations where both plants are vying for the same resource from the environment (Grime 1979). Several species of *Hieracium* including *H. pilosella* have been claimed to be allelopathic (Dawes and Maravolo 1973, Guyot *et al.* 1951, Guyot 1956, Scott 1975, Widera 1978). The experiments presented in this chapter examined allelopathic and competitive relationships between *H. pilosella*, *H. praealtum* and resident tussock grassland species.

In current usage, allelopathy refers to the inhibitory effect of one higher plant on another caused by the escape of toxic substances (allelochemicals) from the former into the environment contiguous with the latter. The most recent reviews of the subject are by Audus (1972), Harper (1977), Muller (1969), Muller and Chou (1972), Rice (1974, 1979) and Whittaker and Feeny (1971). Allelopathy is totally distinct in mode of action from the other form of interference, competition, because it adds a retarding factor

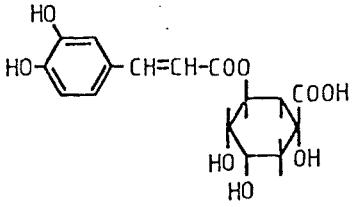
to the environment whereas competition restricts some factor(s) necessary for growth processes. Both forms of interference are defined by plant response. Since this response in both cases is reduced performance, the central task is to discover the causal mechanism. Because of the often identical response to either type of interference and the failure of the experimenter to provide non-circumstantial evidence to link reduced performance with the specific category of interference, almost all claims of allelopathy or competition are not adequately supported. Harper (1977) suggested that symptoms of abnormality which are observable in the field, reproducible experimentally, and are highly specific to a particular type of interference should be investigated in preference to "...qualities as vague as "growth" or "germination"". This view is unjustified since bioassays obviously demonstrate that germination and growth are reliable measures of levels of nutrients or inhibitors under carefully controlled conditions. A better approach is to produce reduced performance and specific symptoms from chemical products of a plant (e.g. Patrick 1970), in which case allelopathy is established.

Although there is no theoretical (Muller 1966, 1969) or logical basis to support such claims, it is not uncommon to find evidence of competition being used to exclude allelopathic explanations of plant suppression (e.g. Kranz and Jacob 1977a, 1977b).

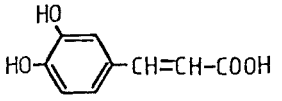
It is reasonable to assume that if two plants are in such close proximity that they are dependent on the same soil volume for water and nutrients then they are also near

enough, in most cases, to be in contact with the biochemical products of each other (Muller 1974). There is no reason why allelopathy and competition should be mutually exclusive relationships. Brief allelopathic action could synergistically enhance competitive advantages or offset them, depending on circumstances.

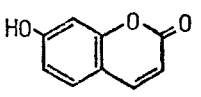
Although volatile compounds predominate in allelopathic relations in arid regions, in moister climatic zones allelochemicals are hydrosoluble and usually phenolic compounds (Whittaker and Feeny 1971, Harborne 1977). Duquenois *et al.* (1956) identified the phenolics present in western European specimens of *H. pilosella* as chlorogenic acid (3-caffeoylquinic acid) caffeic acid (3,4-dihydroxycinnamic acid) and umbelliferone (7-hydroxycoumarin)(Fig. 5.1).



(1) Chlorogenic acid



(2) Caffeic acid



(3) Umbelliferone

Figure 5.1 Structural chemistry of phenols found in *H. pilosella* and *H. praealtum*.

Umbelliferone is present (0.1% W/w) in *H. pilosella* and is commercially extracted for its antibiotic performance against *Brucella arbortus* and *B. melitensis*. Since umbelliferone is a root inhibitor (Garb 1961) and is strongly inhibitory to many species (Dawes and Maravolo 1973, Muller and Chou 1977), a detailed allelopathic investigation was necessary.

Many inappropriate techniques and interpretations are apparent in allelopathic studies, particularly the following:

1. Ecologically or biochemically unsound extraction techniques: Maceration undoubtedly produces reaction compounds in response to cellular disruption (Harbone 1973). Boiling may also radically alter the chemistry of the tissue. Neither technique approaches an ecologically realistic release mode. Ball-milling dead plant parts immediately exposesinternal parts which may not be rapidly available during natural weathering processes.

Allelochemicals are frequently extracted from soils with strong alkali. There is little doubt that many compounds disappear which were probably present and numerous artifacts of degradation are produced (Kaminsky and Muller 1977). Despite the known heat-labile properties of unhydrolysed low molecular weight phenolics (Harbone 1973), the organic phase containing these substances is often dried at high temperature (e.g. McPherson *et al.* 1971 50-60^{o}). Although acetic acid (2%) has been used extensively as a solvent in chromatographic bioassays (Chou and Muller 1972, Gleiessman and Muller 1978, McPherson *et al.* 1971, Wang *et al.* (1967), its property of separating optical isomers

of phenolics (Ribéreau-Gayon 1972) is inappropriate for this purpose but has not been criticised.

2. Test species which are not found in the community: The use of analogues (lettuce bioassay procedures, e.g., McPherson *et al.* 1971) should be condemned. There is no justification for using species which are unlikely to be able to grow in the community and assuming that their responses are approximately the same as resident species. Some resident species, both native and adventive, may be more amenable to experimentation than others due to large seed size, uniform rapid germination, large roots or ubiquity in the field. These species may be preferable to work with and will at least give more relevant information than "exotics".

3. The hierachial approach to determining the limiting factor in plant/environment relationships: In many studies there is an implicit and unfounded assumption that water relations are more important than either nutrient relations or physical and biotic factors, which in turn are supposedly more important than allelopathy. This approach has elements of an infinite regress. It will always be possible to invoke some factor not examined to explain the result non-allelopathically (see Chou and Muller 1972 for a thorough example and Harper 1977 and Wells 1964 for criticisms of this type of work).

4. Donor-receiver designs: These designs are useful for comparing relative effects. However, unless water controls are encorporated in the design (e.g., Scott 1975) they do not provide information on whether a species is inhibitory

in the absolute sense.

5. Soil leaching designs: This type of experiment demands that nutrient levels be monitored and controlled (e.g., Moore and Waid 1971). A negative result is inconclusive since allelochemical production, plant stress and susceptibility to toxins are usually reduced by luxury levels of water (Rice 1974, Muller 1969).

Competition between species can be investigated in a number of ways. One way is by using substitutive or replacement series experiments, an experimental design introduced by de Wit (1960). Performance of each species is assessed in monoculture and in mixtures with each other. Harper (1977) and Trenbath (1978) discuss aspects of the interpretation of this design. Although a variety of numerical measures of aggression or crowding can be calculated from the data, interpretation relies heavily on graphs of yield plotted against density (Z $species_1$ = 0 → 1 and Z $species_2$ = 1 → 0) showing the relative yield per plant in the different situations. This graphical approach has been adopted in this study.

5.2 EXPERIMENTAL

Identification of phenolics

Plant material was collected from Wolds 1 site. Leaf samples were of different types:

(1) green - leaves removed from intact, alive plants immediately before acid hydrolysis,

(2) air dried - green leaves collected in the field and air dried for 3 weeks at 25°,

(3) brown - fully senescent leaves, unleached by rain,

(4) leached - brown leaves after several heavy rainfalls.

Root samples were of two types:

(1) fresh - treated as green leaves above,

(2) dried - treated as air dried leaves above.

Leaf and root samples of 0.1 g (dry weight) were hydrolysed for 30 minutes with 25 ml of 2 N HCl at 100°. The organic material was removed by filtering the extract through Whatman #1 filter paper and the phenolics extracted with three washes of diethyl ether. Anhydrous sodium carbonate was added to remove water present and the combined ether phase taken to dryness in air at room temperature (< 25°) to prevent thermal degradation of labile phenolic compounds. The residue was redissolved in 5 ml of methanol for chromatography and applied in 5 cm width to 25 x 25 cm Whatman #1 chromatography paper. Commercially available standards of chlorogenic acid, caffeic acid and umbelliferone were dissolved in methanol and also applied on each chromatogram to the extract. The phenolics were separated by ascending chromatography in benzene : acetic acid : water (136:72:3). This solvent system is especially useful for phenolic chromatography because the Rf value is related to the number of phenolic hydroxyl groups (Walker 1975). The phenolics were identified by examining the position and colour of bands from the extract and comparing them against the known compounds under:

(a) 360 nm UV light

(b) UV light with ammonia fuming

(c) chromogenic reagents : diazotised p-nitraniline (0.5%) and p-diethylaminoaniline sulfate (0.5%) followed by NaOH(0.1N).

A final check was made by ultraviolet spectroscopy on samples eluted from the chromatograms. Since quantitative analysis of individual phenolics is not highly accurate and involves considerable complexity (Ribéreau-Gayon 1968), a semi-quantitative comparison was made between the same compounds from different plant part sources by comparing the intensities of the spots under UV light.

Surface soils (0-10 cm) were collected monthly (August 1978-April 1979) from Wolds 2 site without removing plants and analysed within 24 h of removal from the field. Plants, stones and coarse organic material were removed using a 4 mm sieve. 1 kg (field moist) of soil was mixed with 1.5 l of distilled water and intermittently stirred for 3 h. The extract was filtered through Whatman #1 filter paper under partial vacuum to remove soil and the extract collected, acidified with a few drops of 5N HCl and the phenolics partitioned into diethyl ether (3X) and analysed as described previously.

Soils were also analysed after the plants were watered in the laboratory. One treatment had all dead leaves removed prior to watering, one had additional dead leaves added to simulate leaf death comparable to the amount occurring at reproduction and one was unaltered. Umbelliferone was estimated from aliquots of leachings and from water on leaf surfaces by reference to standard solutions at the same

pH viewed under 370 nm UV light. This procedure was interference free to about 0.5 ppm (3×10^{-6} M).

Green, brown and leached entire leaves were analysed by placing 0.1 g (dry weight) of each in individual test tubes with 10 ml of distilled water and shaking intermittently for 30 min. The extract was filtered through Whatman #1 filter paper to remove organic residue and treated as described above for chromatography. Umbelliferone was estimated in aqueous solution by reference to standard solutions.

Relative effect of different leaf leachings

Leaf leachings from detached leaves were obtained by placing 2 g (dry weight) of leaves in 100 ml of distilled water and intermittently agitating for 3 h. Three leaf types were used: green, brown and leached. The osmotic pressure of these solutions was measured cryoscopically and the pH measured using pH electrodes. Leachings from growing plants were obtained by repeatedly flushing 100 ml of distilled water through 400 cm^3 pots with four plants of either species grown on Wolds yellow-brown earth from November 1978 to November 1979. *Trifolium repens* seed was germinated in Petri dishes on Whatman #1 filter paper with 25 seeds per dish, replicated 3 times. Each treatment consisted of 15 ml of leachings. Germination and appearance was recorded after 3 days at 20^{o} in light.

Chromatogram bioassay

Aqueous extracts from 1 g of air dried leaves were prepared from *H. pilosella* and *H. praealtum* and chromatography done as described previously except that 3 MM chromatography paper was used to avoid overloading. Rf zones were cut into consecutive 0.1 segments, divided into three parts, and ten *Trifolium repens* seeds placed on each of the three portions in a petri dish. Water was added dropwise to saturate the paper and replenished as required. The appearance of roots on germinated seeds was recorded after 3 days at 20^{o} in light.

Allelopathic effects on roots and growth

The effect of aqueous leachings of *H. pilosella* and *H. praealtum* leaves on seedling roots of eight resident tussock grassland species was assessed in Petri dishes. The species used were: (weeds) *Aira caryophyllea, H. pilosella, H. praealtum, Rumex acetosella, Vulpia bromoides*; (pasture species) *Lolium perenne, Trifolium hybridum* and *T. repens*. 300 mg of air dried leaves were placed beneath Whatman #1 filter paper and 15 ml of distilled water added. Controls were without leaves. Root length was measured with calipers after 14 days at 20^{o} in light.

The effect of *H. pilosella* dead leaves on the growth of *Dactylis glomerata* (cocksfoot), *Trifolium repens* (white clover) and *T. hybridum* (alsike) was studied in a pot trial in the growth room (20^{o}, fluorescent and some tungsten lighting = 180 microeinsteins m^{-2} sec^{-1}).

A low organic matter soil collected from Wolds 1 site

was sieved to remove stones and larger roots, and placed in 10 x 10 cm pots. Seeds of each species were surface sown and well-watered until germination occurred. The seedlings were thinned to 5 similar sized plants per pot with 5 replicates after one week of growth. 1 g of freshly air dried leaves was added to the treatment pots. A second application was made four weeks later. Controls received no additions. The plants were sparingly top watered as required during the experiment. After eight weeks from the first application, plants were harvested for shoots, dried at 80^{o} for 3 days and weighed.

Allelopathic inhibition of new root production of *Festuca novae-zelandiae*

Festuca novae-zelandiae was collected from Wolds 2 site, separated into tillers, washed, and roots excised. Three tillers were held in place with a cotton bung in a 250 ml flask containing 50 ml of 1/1000 strength Bollards solution (Bollard 1966). The flasks were wrapped in black polythene to prevent light reaching the base of the tillers where roots develop. Capillary tubes connected to an air line were inserted into the solution to maintain aerobic conditions.

The treatments were 0, 2, 10, 20 and 100 ppm of umbelliferone with three replicates. The total length of roots produced per treatment was measured with calipers after 21 days in the growth room conditions described above.

Field evidence of allelopathy

A species which produced numerous seedlings most years,

Trifolium dubium (suckling clover), was studied at Cave Stream (see Chapter 3). The density of seedlings inside and outside small *H. pilosella* patches were counted in 50 1 dm^2 quadrats located by a randomised grid procedure. The root length, number of nodules, leaf number and shoot dry weight were obtained from 100 seedlings from each zone.

Competition between *H. pilosella* and *Festuca novae-zelandiae*

Heights of 50 *Festuca novae-zelandiae* tussocks outside and within almost pure *H. pilosella* patches about 10 m across were measured at Wolds 2 site.

Nitrogen and phosphorus contents were determined from three bulked samples of green leaves from twelve tussocks in each area which were dried at 80^{o} for three days and ball-milled to a fine powder. 0.1 g samples were digested in 10 ml of sulphuric acid - hydrogen perioxide reagent (Allen *et al.* 1974 p.89). Total nitrogen was estimated by the semi-micro Kjeldahl method (Bremner 1965) and phosphorus by the molybdenum-blue colorimetric method (Allen *et al.* 1974).

Competition between *H. pilosella* and *F. novae-zelandiae* was examined in a glasshouse competition experiment. Plants of both species were collected from Wolds 2 site and grown in 10 x 10 cm pots containing 700 cm^3 of a yellow brown earth from the same site in a replacement series design with two plants per pot. The species proportions were:

(1) two *H. pilosella* plants,

(2) one *H. pilosella* plant and one 3-tiller *Festuca zelandiae* plant,

(3) two plants of the latter species.

The plants were spaced 5 cm apart. The tussock was extablished in August 1975. There were six replicates of each and the plants were grown together from January to October 1976. Leachings from soils containing *H. pilosella* were examined for umbelliferone as previously described at the end of this period. The shoots were then harvested, dried at 80^{o} for 3 days and weighed.

Samples of green leaves from each replicate were taken and combined to form two composite samples per species per planting proportion and analysed for nitrogen and phosphorus as before.

Competition between *Hieracium* and pasture species

Two-species competition under different moisture and soil fertility conditions was studied using a replacement series design in a glasshouse pot trial. *H. pilosella* and *H. praealtum* were grown from plants collected from colonies on Wolds 2 site. Pasture species were grown from seed. The clovers, *Trifolium repens* and *T. hybridum*, were inoculated with *Rhizobium*. Seed was germinated in Petri dishes on moist filter paper and potted at about 14 days from germination with the hawkweeds in November 1978 in 4:0, 3:1, 2:2, 1:3 and 0:4 species proportions. Initially the plants received regular watering as required. In February the pots were separated into three treatments, a control receiving regular watering and fertiliser amendment; a lower fertility treatment, with regular watering and no amendment; and a low watering treatment with fertiliser amendment but reduced watering.

On 6 February 1979, 0.14 g Mo-superphosphate per pot was added to the control and low watering treatment pots. Reduced watering was imposed on the latter treatment on 25 February 1979, and adjusted to prevent permanent wilting. A further fertiliser amendment of 0.07 g each of Mo-superphosphate and calcium nitrate (26% N) was made on 23 March to the control and low watering treatments. Watering was discontinued for 14 days in the low watering treatment on 26 March and resumed on 9 April. Shoots were harvested on 3 May, dried at 80^{o} for 3 days and weighed. Leachings from soils in pots containing *H. pilosella* were examined for umbelliferone as before.

5.3 RESULTS

Allelopathy

Chlorogenic acid (3-caffeoylquinic acid) and caffeic acid (3, 4-dihydroxycinnamic acid), phenolics of the cinnamic acids group (Harborne 1973), were identified in extracts from living leaves and roots of *H. pilosella* and *H. praealtum* (Tables 5.1 and 5.2, Fig. 5.1). *H. pilosella* leaves also contained the phenolic umbelliferone (7-hydroxycoumarin), a coumarin. Umbelliferone was specific to *H. pilosella* leaves. The other phenolics, while present in roots, were more concentrated in leaves, and equal amounts occurred in equivalent parts of both species. Dead unleached leaves and detached air dried leaves contained the same phenolics in similar amounts to living leaves. Dead leached leaves were free of phenolics.

Water extracts of dead unleached leaves and detached

TABLE 5.1 Phenolic compounds[1] found in plant, parts water extracts, and soils of *H. pilosella* and *H. praealtum*

	Chlorogenic acid		Caffeic acid		Umbelliferone	
	H. pilosella	*H. praealtum*	*H. pilosella*	*H. praealtum*	*H. pilosella*	*H. praealtum*
leaves: living - green	+	+	+	+	+	-
dead - attached, unleached	+	+	+	+	+	-
dead - attached, leached	-	-	-	-	-	-
dead - detached, air dried	+	+	+	+	+	-
Water extracts of leaves: - green	-	-	-	-	-	-
Water extracts of leaves: - attached, unleached	+	+	+	+	+	-
Water extracts of leaves: - attached, leached	-	-	-	-	-	-
Water extracts of leaves: - detached, air dried	+	+	+	+	+	-
roots: - living	+	+	+	+	-	-
roots: - dead	+	+	+	+	-	-
soils: (August - mid April)	-	-	-	-	-	-
Soils - after plants watered:						
- no dead leaves present	-	-	-	-	-	-
- some dead leaves present	t	t	t	t	+[2]	-
- many dead leaves	+	+	+	+	+[3]	-

[1] + present
t trace
- absent

[2] c. 5×10^{-6} M

[3] c. 3×10^{-5} M : 3×10^{-4} M on leaf surface

Table 5.2 Chromatographic characteristics of phenolics from *H. pilosella*, and *H. praealtum*

Characteristic	Chlorogenic acid	Caffic acid	Umbelliferone[1]
Rf - observed	0.05	0.28	0.69
Rf - standard	0.05	0.28	0.70
Colour - UV	blue	blue	light blue
" UV + NH_3	green	blue-green	light blue
" diazotised - p-nitraniline	green-yellow	grey-green	tan
" p-diethlamine aniline sulphate	green	light blue	light blue & fluorescent
" EtoH max. (nm)	245, 300, 330	243, 326	325 inflection at 340

1. *H. pilosella* leaves only

air dried leaves contained the phenolics originally present in the leaves. No phenolics were removed from living leaves by water extraction.

Field soils collected at monthly intervals from August 1978 to mid April 1979 did not contain detectable phenolics. The same soils analysed after some watering of *Hieracium* plants had traces of phenolics except when dead leaves were removed before watering, demonstrating that the roots were not the phenolic source. Higher levels of phenolics were found in soil which had many dead unleached leaves present on the surface.

The bioassay of various water extracts on the interim germination of *Trifolium repens* seeds showed that the maximum inhibition was from dead but previously unleached leaves (Table 5.3). Minimum inhibition was from extracts from living leaves in accordance with the phenol determinations (Table 5.1). Extracts from dead unleached leaves of both species showed significant inhibition of *T. repens* germination though this inhibition was greater from *H. pilosella* extracts and extended also to extracts from partially leached leaves. Morphological abnormalities were observed including apical abnormality, stele exposure and absence of hairs (plate 5.1).

In the second bioassay where *T. repens* seed was germinated on 0.1 Rf segments of chromatograms of water extracts from freshly air dried leaves of *H. pilosella* and *H. praealtum*, root damage (apical abnormality, stele exposure) was confined to Rf zones 0-0.3 with *H. praealtum* and 0-0.3 and 0.5-0.7 with *H. pilosella*. These zones contained all the phenolics Table (5.2).

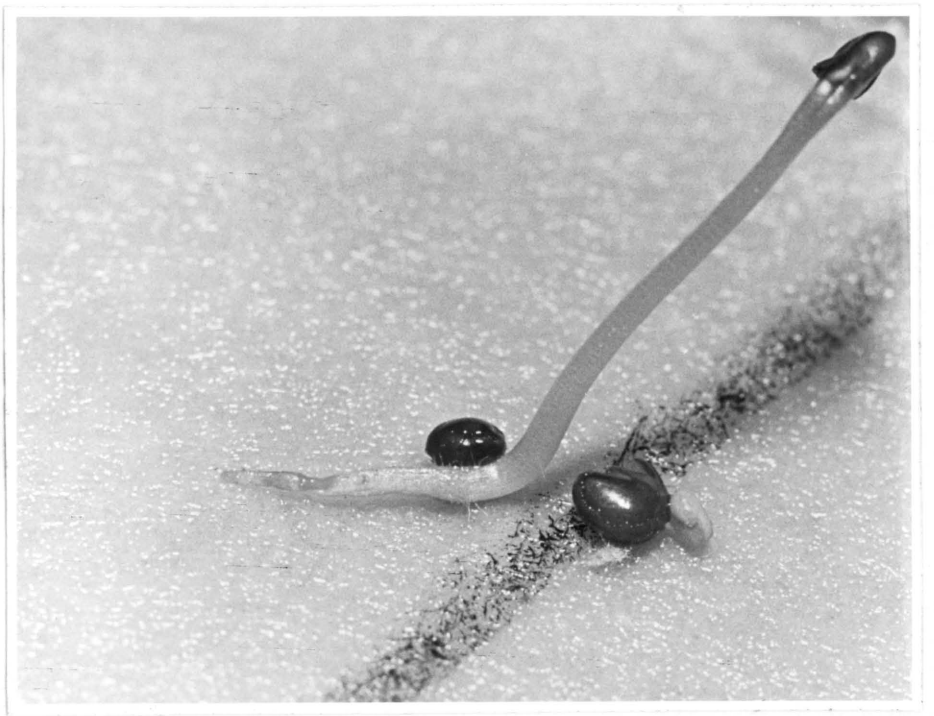


Plate 5.1 The abnormal radicle morphology (absence of root hairs, exposed stele and damaged apex) of *T. repens* germinated with *H. pilosella* dried leaf extract.

TABLE 5.3 Means and ANOVA of effect of various water extracts of *H. pilosella* and *H. praealtum* on interim (3 days) germination percentage of *Trifolium repens*

Extract	*H. pilosella*	*H. praealtum*
Dead unleached leaf[1]	45.2 a	65.2 bc
Dead partially leached leaf	60.0 b	78.8 cde
Soil beneath	72.0 bcd	85.2 de
Living leaf	86.8 de	90.8 e
Soil	76.0 cde	
Distilled water	88.0 de	
1 pH	6.3	6.2
Osmotic concentration (bars)	0.4	0.7

ANOVA

Sv	df	MS	F
Between extracts	9	39.14	8.7***
Within extracts	20	4.50	

The petri dish experiment showed that extracts of *H. pilosella* leaves were generally strongly inhibitory to root growth of all species tested (Table 5.4). This inhibition was maximum against its own roots (auto-allelopathic) and *Vulpia bromoides* and least against *T. hybridum*. Also, *H. praealtum* was significantly inhibitory against *Vulpia bromoides* and *H. pilosella* root growth. *H. pilosella* caused phytotoxic symptoms of apical browning, absence of root hairs and tissue damage.

In the solution culture experiment of root growth, *Festuca novae-zelandiae* was strongly inhibited by low levels of umbelliferone in a linear manner (Fig. 5.2) Complete suppression of growth was estimated to occur at about 22 ppm (1.4×10^{-4} M) umbelliferone in solution.

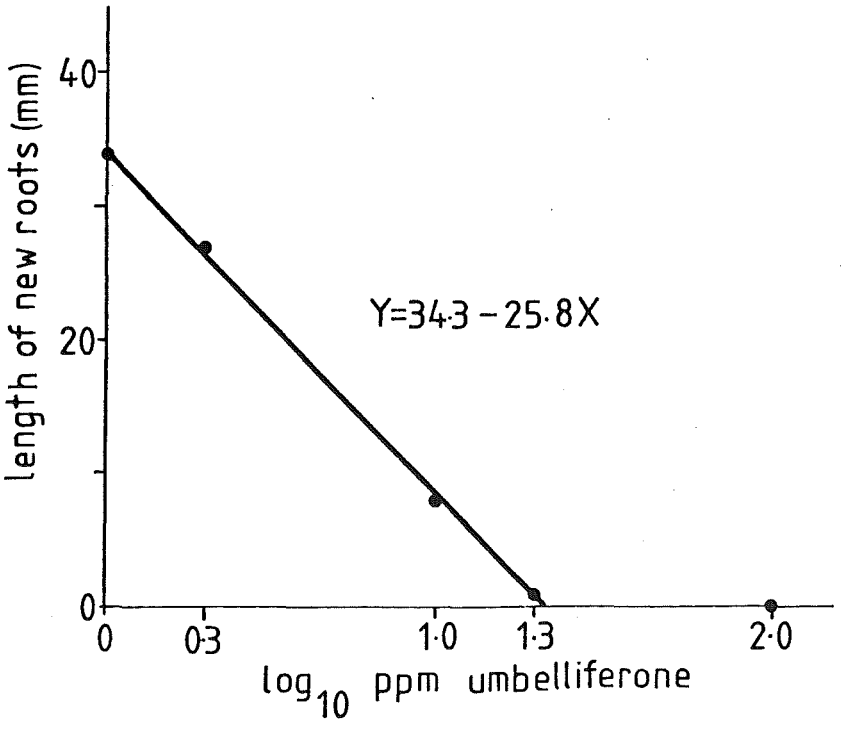


Figure 5.2 The relationship between umbelliferone concentration and root growth of *Festuca novae-zelandiae* in water culture.

Table 5.4 Treatment means and ANOVA of aqueous leachings of *H. pilosella* and *H. praealtum* on root growth of eight species seedlings after 14 days. Means $\log_e$ (mm) with arithmetic mean in brackets

Species	Control	*H. pilosella* 0.4 bar	*H. praealtum* 0.7 bar
Hieracium pilosella	3.00 (19.6) a	1.12 (2.2) c	2.53 (12.1) b
H. praealtum	2.93 (18.3) a	1.65 (4.6) b	3.09 (21.4) a
Vulpia bromoides	3.49 (32.8) a	1.80 (5.7) c	2.76 (15.4) b
Aira caryophyllea	2.72 (14.5) a	0.67 (1.1) b	2.77 (15.8) a
Lolium perenne	4.34 (78.9) a	3.04 (21.3) b	4.18 (66.3) a
Rumex acetosella	3.14 (22.5) a	2.00 (7.1) b	3.19 (24.0) a
Trifolium hybridum	2.55 (12.4) a	2.58 (12.7) b	2.82 (16.5) a
T. repens	2.58 (12.5) a	2.18 (8.1) b	2.46 (11.0) a
Mean	3.09	1.88	2.98

ANOVA

Sv	df	MS	F
Leachings	2	71.94	861***
Species	7	17.80	213***
L x S	14	3.32	40***
Error	456	.08	

In the pot trial on three pasture species, the addition of dried *H. pilosella* leaves significantly depressed the seedling growth of *Dactylis glomerata* and *T. repens* (Table 5.5). The trend was for *H. pilosella* leaves to promote the seedling growth of *T. hybridum*, but the effect was not significant.

In the field assessment, four of the five seedling characteristics of *Trifolium dubium* were reduced within *H. pilosella* colonies (Table 5.6). Apex necrosis and scarring from cortical damage were found on 52% and 10% respectively of the seedlings. Similar symptoms were seen in *T. arvense*.

Competition

In the field at the Cave Stream site, *Festuca novae-zelandiae* tussocks growing within *H. pilosella* colonies were shorter than those in other vegetation (Table 5.7). Nutrient analyses of green leaves of *F. novae-zelandiae* from the plants within *H. pilosella* colonies were lower in nitrogen and phosphorus content than from tussocks away from *H. pilosella*.

The first glasshouse experiment showed competitive interaction between *H. pilosella* and *Festuca novae-zelandiae* (Fig. 5.3). The yield of *F. novae-zelandiae* plants was reduced to 26% of expectation in the z = 0.5 mixture relative to the monoculture. The total yield of *H. pilosella* was similar in both monoculture and competition. Phosphorus foliage content was halved when in competition with *H. pilosella* (Table 5.8). No traces of umbelliferone were found in soils which contained *H. pilosella*.

Table 5.5 Shoot weight (mg per pot) of three species in relation to the presence of *H. pilosella* leaves in pot trial (n = 5)

Species	*H. pilosella* leaves		t test
	Absent	Present	
Dactylis glomerata	412 ± 140	76 ± 83	4.6 ***
Trifolium repens	229 ± 100	85 ± 35	3.0 *
T. hybridum	153 ± 61	214 ± 151	0.8 ns

Table 5.6 Allelopathic effects of *H. pilosella* and *Trifolium dubium* seedlings at Cave Stream site (n = 100).

Characteristic	*H. pilosella* colonies		t' test
	Within	Outside	
Density (No dm^{-2})	0.7 ± 1.6	9.9 ± 11.9	7.7 ***
Shoot dry weight (mg)	60 ± 23	190 ± 94	13.4 ***
Root length (mm)	16 ± 7	29 ± 9	11.4 ***
Leaf number	2.1 ± .7	3.4 ± 1.1	10.0 ***
Nodules (No mm^{-2})	0.08 ± .07	0.07 ± .05	1.2 ns

Table 5.7 Height, nitrogen and phosphorus content of *Festuca novae-zelandiae* foliage in relation to *H. pilosella* colonies at Cave Stream.

Parameter	*n	*H. pilosella* colonies		t test
		Within	Outside	
Height (cm)	25	23 ± 8	40 ± 9	7.7***
% N	3	1.14±0.1	1.53±.06	11.1***
% P	3	.23±.02	.31±.02	4.9

Table 5.8 Nitrogen and phosphorus content of *H. pilosella* and *Festuca novae-zelandiae* in glasshouse pot trial (n = 3)

Parameter & species		Monoculture (z = 1.0)	Competition (z = 0.5)	t test
% N	*H. pilosella*	1.17 ± 0.24	1.33 ± 0.28	0.5 ns
	F. novae-zelandiae	.64 ± .18	.58 ± .14	0.9 ns
% P	*H. pilosella*	.12 ± .01	.12 ± .01	0 ns
	F. novae-zelandiae	.13 ± .01	.06 ± .01	9.9 ***

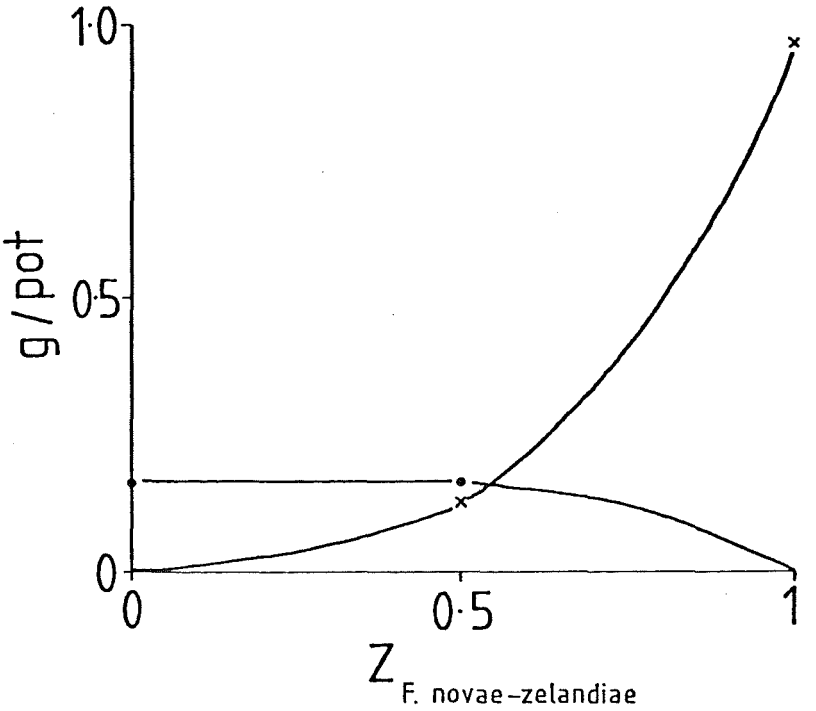


Figure 5.3 The yield of *Festuca novae-zelandiae* (x) and *H. pilosella* (●) in a replacement series competition experiment

In the competition experiment involving two-species mixtures of hawkweeds and pasture grasses or clovers in a replacement series, the root systems were completely intergrown and could not be separated so that results refer to shoots only (Fig. 5.4).

Although monoculture yields of *H. pilosella* and *H. praealtum* were inferior to the other species used (except *L. perenne*) under the control treatment, they generally were equal or better than the pasture species under low water/fertility conditions. *H. pilosella* grew slightly better in the presence of *D. glomerata* and *L. perenne* under low water conditions than predicted from the replacement ratio. *H. praealtum* suppressed *T. repens* at low fertility. *H. pilosella* grew better with *T. repens*, especially in the low water and low fertility treatments. *T. hybridum* suppressed *H. pilosella* in the control treatment. *T. hybridum* died back more severely in the monoculture pot than in the

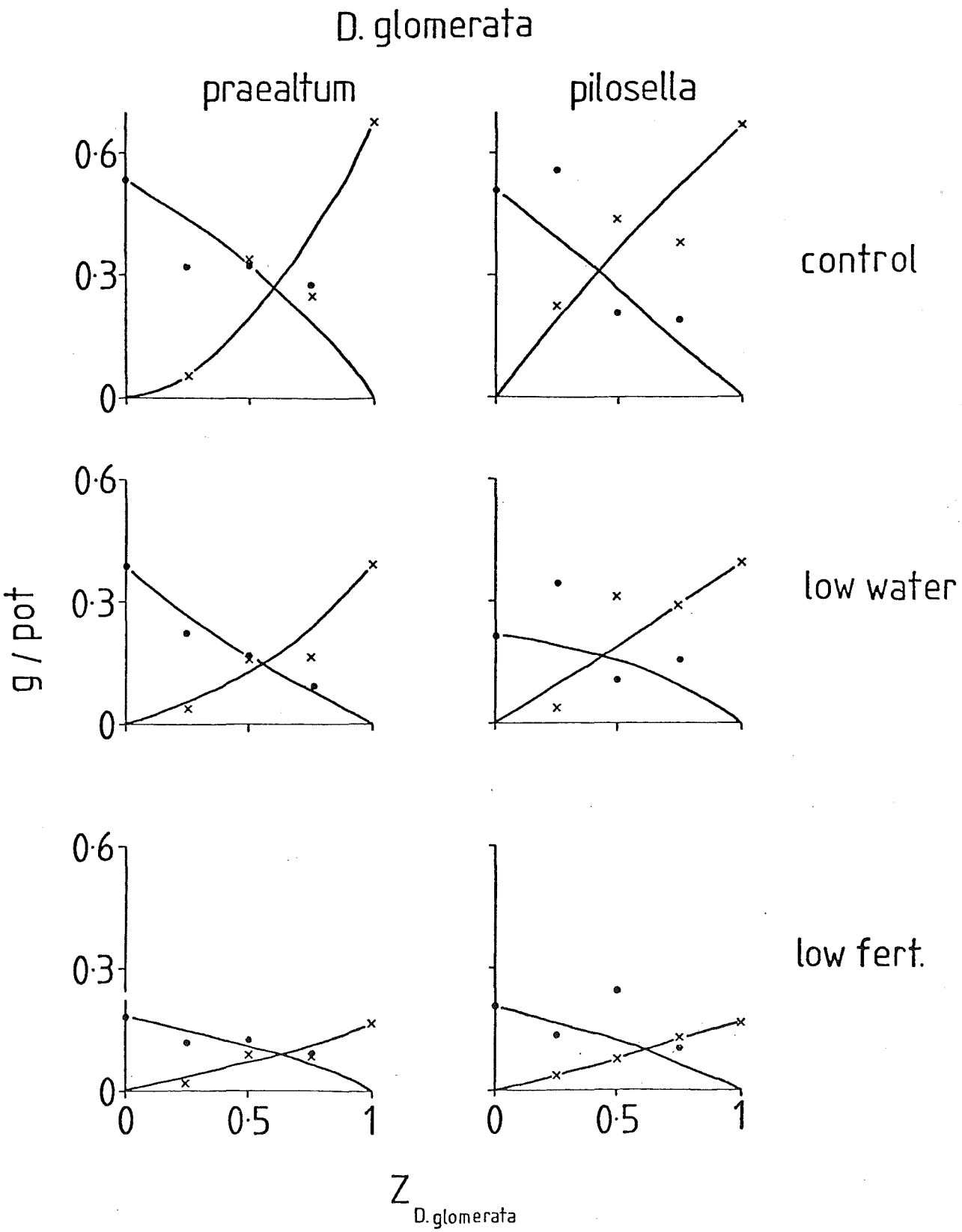
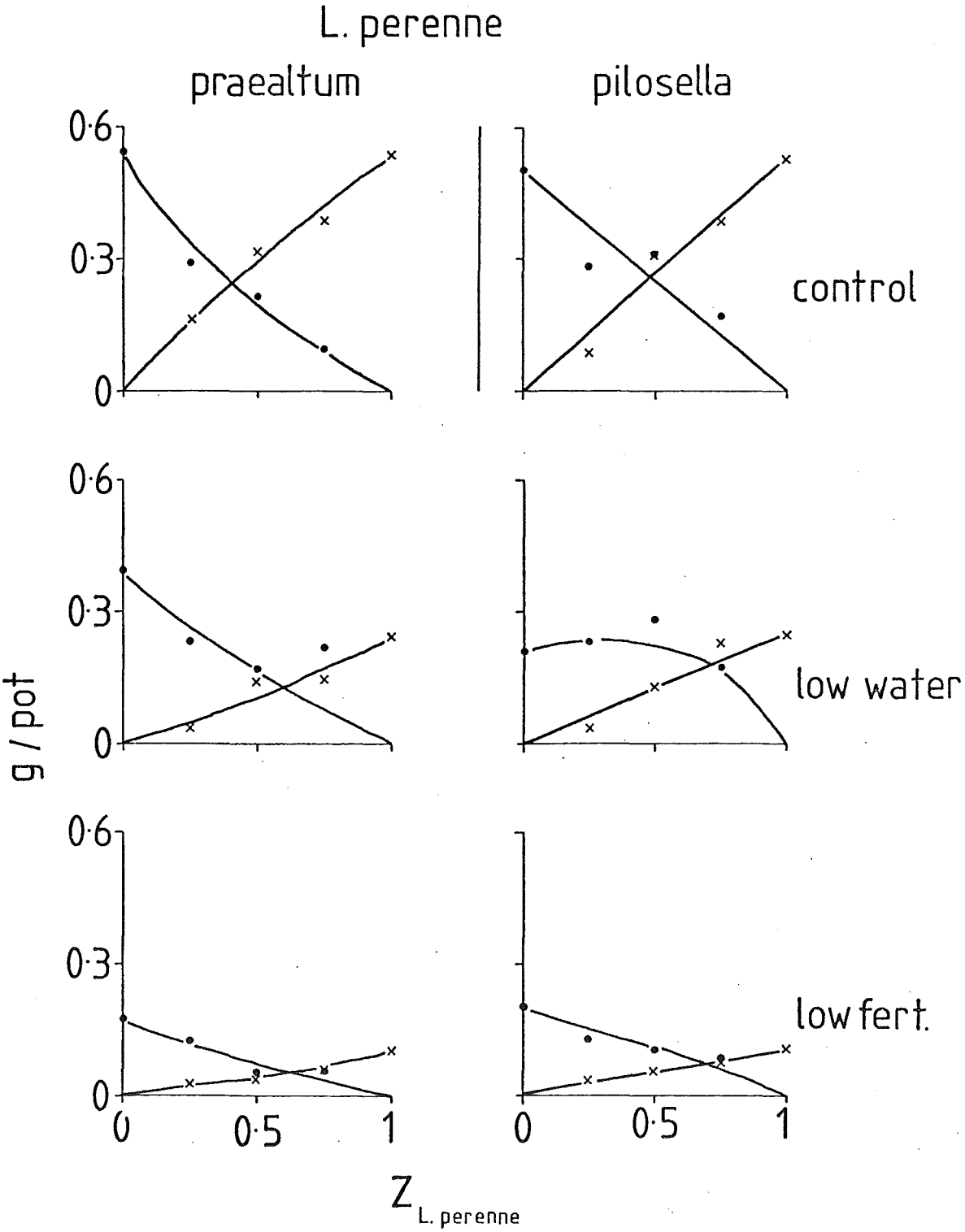
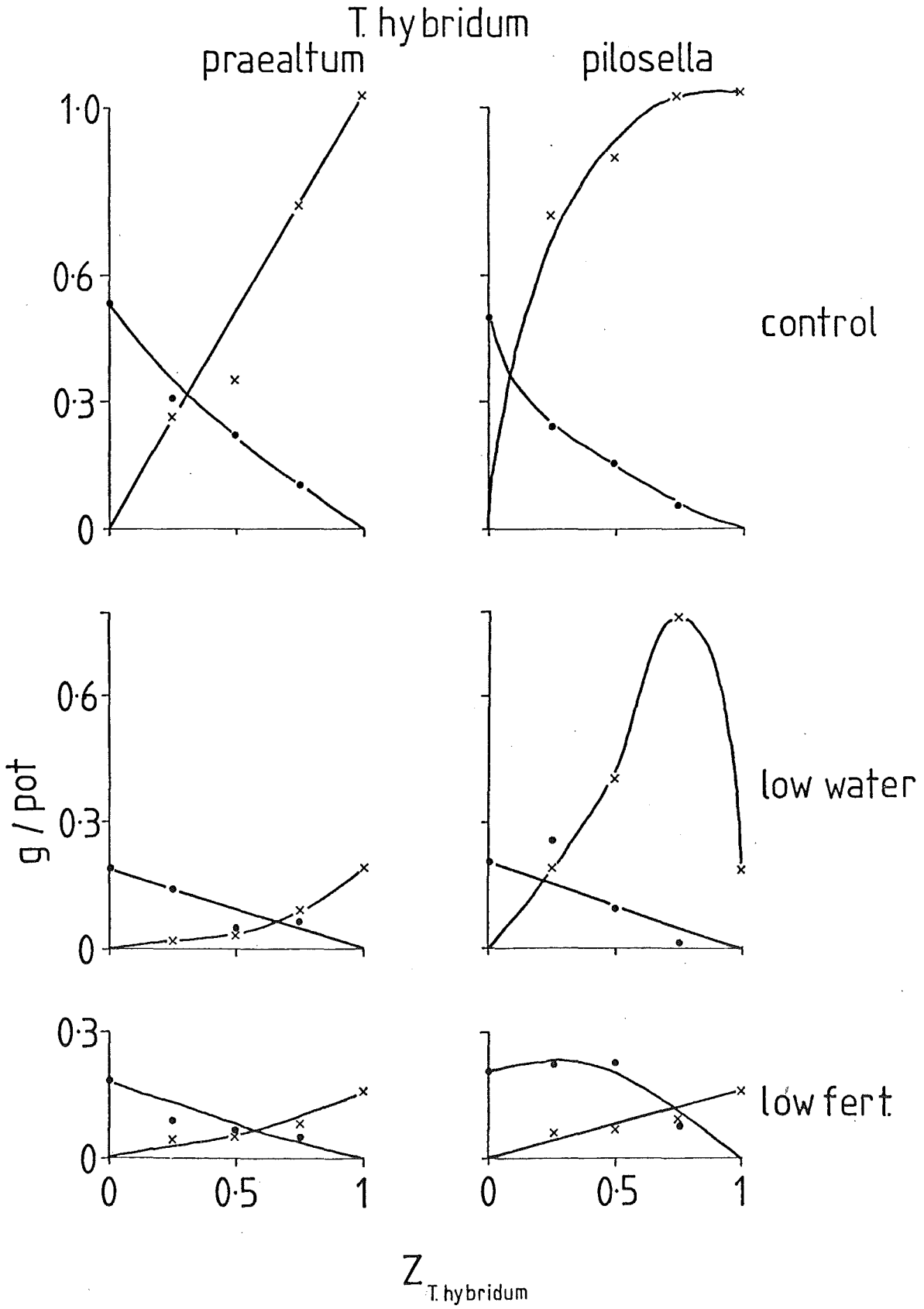


Figure 5.4 The yield of pasture grasses and legumes (x) and *Hieracium* species(●) in a replacement series competition experiment.


L. perenne
praealtum
pilosella
0·6
0·3
0
control
low water
low fert.
g / pot
0
0·5
1
Z L. perenne


T. hybridum
praealtum
pilosella
1·0
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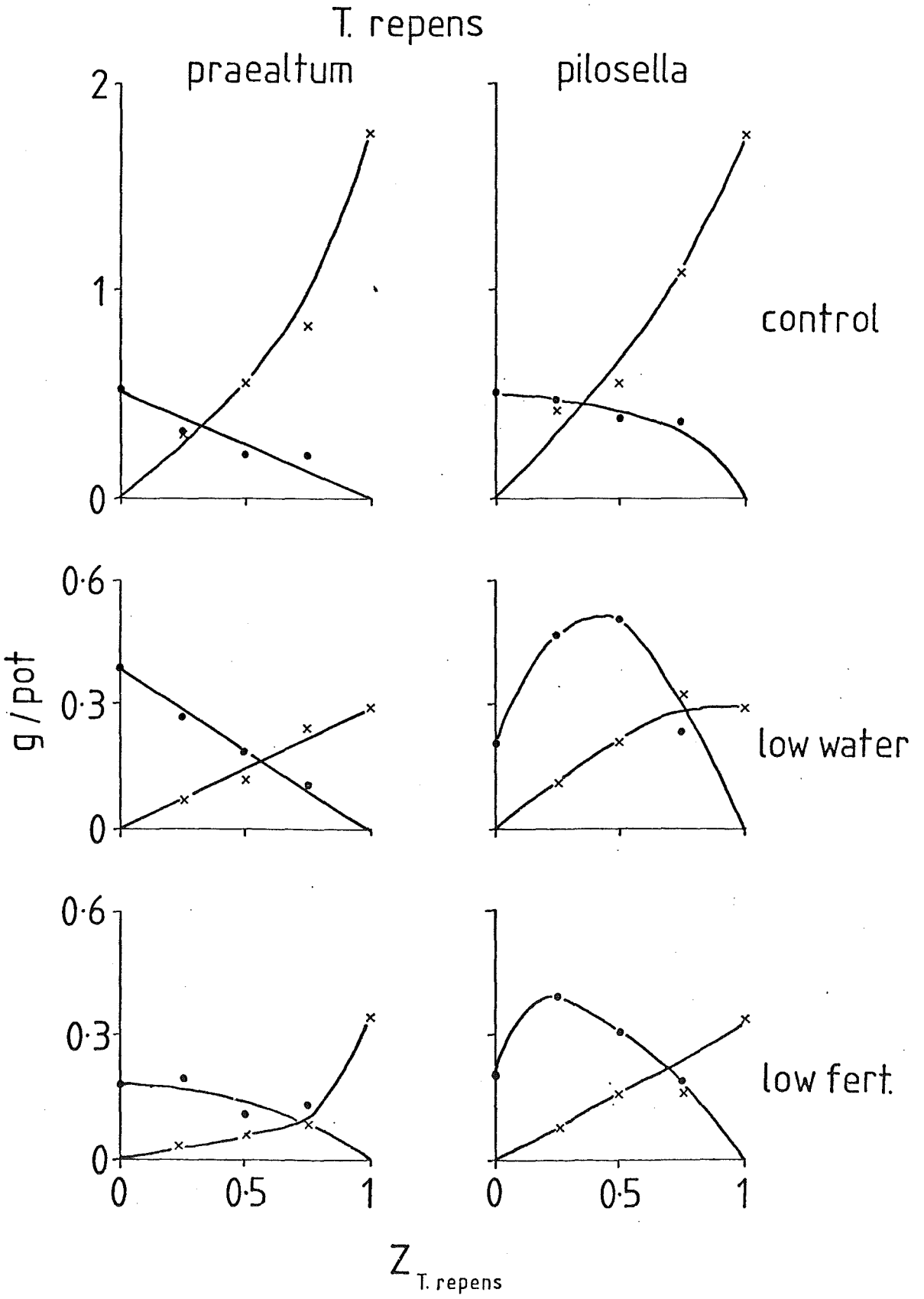
0·3
0
control
low water
low fert.
g / pot
0·5
1
Z T. hybridum


T. repens
praealtum
pilosella
2
1
0
control
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g / pot
low water
0·6
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0
low fert.
0
0·5
1
0
0·5
1
Z T. repens

replacement pots with *H. pilosella*. *H. pilosella* grew better with *T. hybridum* at low fertility. No traces of umbelliferone were found in *H. pilosella* soils.

5.4 DISCUSSION

The results have shown that dead *H. pilosella* leaves initially contained water soluble substances which were freely leached, producing considerable inhibition of interim germination, growth and symptoms of abnormality to roots on all species tested except *T. hybridum*. Germination and growth inhibition, absence of root hairs, tissue damage and apical browning were observed and these are characteristic symptoms of phytoxicity (Patrick 1971). In contrast, *H. praealtum* leachings were almost without effect, except for two cases of moderate growth inhibition. Although other results have shown that allelopathic effects on the interim germination of *T. repens* and other pasture species were maximal and decrease by final germination (Macfarlane 1980, Scott 1975), any condition which inhibits the emergence of the radicle or reduces its penetration into the soil will increase establishment failure (McWilliam *et al.* 1970) especially in a stressful environment. The inhibitory effects and root abnormalities were traced principally to the coumarin, umbelliferone, which only occurred in *H. pilosella* leaves. No evidence was obtained which would indicate that any phenolic compound was able to leave the plants in detectable quantities except from dead leaves. The roots do not, even in the laboratory, actively or passively release phenolics. Consequently most of the

allelopathic activity would be initially concentrated near the dead leaves. Field evidence supported this finding. Although seedling inhibition and damage to recently germinated *T. dubium* and *T. arvense* was found, no symptomatic evidence of allelopathy on mature plants was discovered, presumably because the growing roots were below the allelopathic zone. Growth room experiments on *T. repens* and *D. glomerata* seedlings clearly showed that young seedlings may be vulnerable. It is postulated that the lack of inhibition in *T. hybridum* seedlings was due to the resistance to root inhibition from *H. pilosella* dead leaf products based on the root inhibition experiment.

Despite the absence of phenolics in the soil during regular field sampling, it was possible to detect them in the same soils if newly dead leaves were present on the surface and these were eluted. This result suggests that allelochemical appearance is irregular and very transitory in the field soil situation.

The concentration of umbelliferone estimated in the soil solution was initially about 5 ppm or 3.1×10^{-5} M (Table 5.1), a level which produced 50% inhibition of new root growth on *F. novae-zelandiae* (Fig. 5.2). This soil solution concentration was based on the assumption that umbelliferone was evenly distributed, which is unlikely (Guenzi and McCalla 1966, Patrick 1971). Furthermore, low organic matter soils containing clays can cause re-concentration of phenolics by a process similar to column chromatography (Muller and Chou 1972).

According to the criteria discussed in the Introduction,

the results presented have established a strong case for allelopathy being one of the modes whereby *H. pilosella*, and to a lesser extent *H. praealtum*, interfere with other species. The causal basis for allelopathic interference was not examined. However, the coumarins are noted for their ability to interfere with normal mitotic activity in the root meristem (Avers and Goodwin 1956). A level of 2.5×10^{-4} M of 4-methyl umbelliferone caused 20% of mitosis in onion roots to be aberrant. Mitostasis occurred at about 5×10^{-4} - 1×10^{-3} M (D'Amato and D'Amato-Aranzi 1954). The effects also continued after the coumarin solution was replaced by water. The levels of umbelliferone on moist leaf surfaces was about these quantities. Equally low levels of phenolic acids, particularly cinnamic acids (including caffeic acid) have been shown to inhibit phosphate uptake in barley (Glass 1973).

H. pilosella appeared to suppress *F. novae-zelandiae* growing in the field. *F. novae-zelandiae* had less nitrogen and phosphorus when growing in *H. pilosella* colonies. A glasshouse pot trial confirmed the suppression hypothesis. Although according to the definition in the Introduction the pot replacement series experiments have only established interference between *Hieracium* and other species, the absence of umbelliferone in soils suggests that the interference was through competition for some environmental factor. Although *H. pilosella* did not derive a nutrient advantage in terms of nitrogen and phosphorus in excess of increased yield when grown with *F. novae-zelandiae*, the latter had a phosphorus deficiency.

Since *H. pilosella* reduces the available phosphorus in the surface soil in older patches (Table 3.9) the nutritional problems of the tussock are probably worse over a longer period than measured in this experiment. Recent work suggests that phosphorus nutrition/allelopathy interactions may explain some instances of single species dominance in grasslands (Newman and Miller 1977).

H. praealtum was not superior in mixture to the pasture species tested except against *T. repens* under low fertility conditions. This result may be a reflection of the low fertility tolerance of *H. praealtum* relative to *T. repens*. *H. pilosella* was superior under low water conditions against both grasses and *T. repens*, but not *T. hybridum* which is more drought tolerant than the other clover. These results are consistent with the apparent dry habitat preferences of *H. pilosella*. The better growth of *H. pilosella* against both *T. repens* and *T. hybridum* at low fertility is interesting. *H. pilosella* had higher soil fertility preferences than *H. praealtum* and could be expected to do less well than the latter at low fertility. It is possible that nitrogen fixation by the clovers raised the local soil fertility which would benefit *H. pilosella* more than *H. praealtum*.

T. hybridum suppressed *H. pilosella* under control conditions by overgrowth. *H. praealtum* responded better to this situation due to its normally taller, erect habit and greater leaf extension when shaded (Table 4.5). However, *T. repens* was more restricted in height by its stoloniferous habit and grew around but did not overgrow

plants of *H. pilosella* which performed well.

H. pilosella emerged as a plant with considerable interference potential in the experiments. However an agronomically important species *T. hybridum*, was resistant to allelopathy and able to overgrow *H. pilosella* under conditions of improved soil fertility and adequate moisture.

CHAPTER 6

PHYTOSOCIOLOGY OF *HIERACIUM* IN RELATION TO AGRICULTURAL DEVELOPMENT

6.1 INTRODUCTION

The theme of the present study has been to assess the biology of *Hieracium pilosella* and *H. praealtum* in relation to their weed threat to the pastoral agriculture of the tussock grasslands. Other agencies have been undertaking agricultural type trials on *Hieracium* control. In particular, Grasslands Division, DSIR, established trials in an area initially low in *Hieracium* (Ruataniwha site, Chapter 3) and already dense *Hieracium* (Sawdon site), to investigate the effect of different fertiliser and pasture species inputs combined with grazing in different seasons of the year. The opportunity was taken to use these trials for phytosociological studies on the place of *H. pilosella* and *H. praealtum* in the vegetation at the start of the trial, and the change of the *Hieracium* component during the first three years under the different treatments.

Quantitative or semi-quantitative measurement of species composition in tussock communities is complicated by the large number of species of different growth forms. For this reason cover, although rapidly estimated, is not equally related to the biomass of all species (Scott 1965). Furthermore, the inherently high sampling variance in phytosociological data does not justify high precision in measurement. Variance can be lowered more efficiently by increasing the size of the sample (Goodall 1970). Ranking

methods provide a rapid method of biomass estimation (Goodall 1970, Scott and Maunsell 1974) with high monotonic accuracy (Mannetje and Haydock 1963).

Further, by reverse ranking, i.e. assigning high value ranks to the more abundant species, it is possible to get pseudovalues directly related to biomass estimates. Anderberg (1973) empirically demonstrated that ordinal data of this form have a good correlation with their original interval scale values for input to multivariate analyses provided the number of ranks used were less than fifteen.

A description of the association between the species in a community can be obtained from their joint occurrence or non-occurrence in quadrats, with such descriptive association possibly leading to understanding of functional associations. Principal factor analysis is one method of analysis for determining association where there is a quantitative or semi-quantitative measure of the species in each quadrat and no *a priori* assumption of the form of the association. These conditions appeared to apply to quadrat ranking data. Factor analysis explains the variance of multivariate data in terms of new and fewer components than in the original data (Dagnelie 1975). Each successive factor accounts for the maximum common variance while still remaining uncorrelated with preceding factors (Harris 1975). Ideally it is possible to express the important information contained by a high dimensional set of data in a low dimensional simple structure (e.g. Streibig 1979). In practice it is assumed that it will be possible to give biological meaning to the factors so defined (Scott 1969).

In common with multivariate procedures developed from parametric theory, principal factor analysis was intended for continuous interval data. However recent mathematical and empirical evidence indicates that this procedure, along with most other multivariate techniques, is robust under violation of normality and homoscedasticity assumptions (Harris 1975).

Plant communities are comprised of mixtures of differentially successful species. These species can be ordered sequentially from the most to the least important members on the basis of selected attributes (e.g. productivity, biomass, number of individuals, area of ground cover) (Whittaker 1965). These communal series of values plotted logarithmically are known as dominance-diversity curves, and vary in form according to the numbers of species (viz. diversity) and their importance (niche) within the community.

Whittaker (*loc. cit.*) has examined the form of dominance-diversity curves for a range of vascular plant communities in relation to hypothetical models of competition for niche space. In the first model, the community has a small group of dominants, a large intermediate group of co-dominants and a small group of rare components. Communities of this type give rise to curvilinear dominance-diversity graphs and are assumed to be the outcome of no single species having a marked competitive advantage over the others. In the second model, it is assumed that the most important species can obtain a fixed fraction of the total niche space, the next most important species the

same fraction of the remaining space and so on according to a geometric progression. Thus, most of the vegetation is comprised of a few species. This second model describes the "niche pre-emptive" situation and leads to the linear dominance-diversity relationship (Whittaker *loc.cit.*).

The changes in vegetation through time, either as part of natural succession, or through applied treatments, can be monitored by repeated sampling of permanent quadrats. Recently the statistical treatment of such vegetation data has been improved by the use of the transition matrix or Leslie matrix model developed in zoological studies (e.g. Enright and Ogden 1979, Van Hulst 1979). This approach is most applicable where the data is ordinal, and there is a large number of quadrats, measured at regular time intervals, so that given the state at one stage (e.g. presence of species A), the data can be used to determine the probability of another state (e.g. increase of species B and decrease of species A) at a subsequent time interval. This approach was used to appraise its usefulness in agricultural type trials using rank vegetation measurements. The potential value of the approach is the prediction of long term trends (Debussche *et al.* 1977, Van Hulst 1979).

6.2 EXPERIMENTAL

The general site details and vegetation descriptions of Ruataniwha and Sawdon site used were previously presented (Chapter 3). *H. pilosella* was in the early stage of colony development at the Ruataniwha site. Initial visual estimates of cover as a percentage of vegetation were 15%

for *H. pilosella* and 10% for *H. praealtum*. At the Sawdon site *H. pilosella* was at an advanced stage of colony formation, amounting to 70% of the vegetation. *H. praealtum* was rare.

Within these two general areas a trial had been established in spring 1975 of 12 0.25 ha fenced paddocks. Eight paddocks (developed) at each site had been overdrilled with a range of pasture legumes and grasses in various combinations together with annual fertiliser of 200 kg ha^{-1} 400 S Mo superphosphate. Four paddocks (undeveloped) were not modified. Sets of two developed paddocks and one undeveloped paddock were subjected to three different seasonal grazings of either grazing during spring (September-December), or summer/autumn (January-April), or winter (May-August). The two remaining developed paddocks were rotationally mob stocked as required, while the remaining undeveloped paddock was ungrazed from 1975. The rate of stocking was adjusted to utilize the herbage available within the grazing period.

Sampling was done at 30 permanent positions per paddock located along three diagonal lines. The species occurring within 1 m^2 quadrats were visually assessed and the top ten species ranked in terms of shoot biomass (10 = most biomass .. 1 = least). The remaining species present were listed and given an arbitrary value of 0.2. Sampling was done during November 1975 and December/January 1978/9.

In relation to the results presented, establishment of the overdrilled species was negligible at the first sampling at the Ruataniwha site in 1975, and sparse at the Sawdon site. Also the eight developed paddocks at the

Sawdon site were similar in the good establishment and spread of the clovers *Trifolium hybridum*, *T. repens* and *T. pratense* by 1975 and low establishment of other sown legumes and grasses. The three clovers showed much slower establishment and spread at the Ruataniwha site.

Principal factor analysis was employed on the November 1975 data from the undeveloped paddocks using only the species present in 5% or more of the quadrats. The method used was principal factor analysis according to Nie *et al.* (1975) with a varimax iterative solution using a minimum eigenvalue of 1.0.

The transition matrices were calculated from the changes between the November 1975 and the December/January 1978 measurements.

Seed production of *H. pilosella* and *H. praealtum* was determined by procedures described earlier (Chapter 3) from 50 x 1 m^2 transects in the spring and summer grazed blocks of the developed series and the summer grazed block of the undeveloped series during the inflorescence formation and seed dispersal period. The entire spring grazed undeveloped block was sampled. Seed output and sites available for colonisation by seed were negligible at Sawdon which was not sampled.

6.3 RESULTS

Species ranking

The mean ranking of species at the two sites in November of the first year is given in Table 6.1. Both sites had a diverse flora. *Festuca novae-zelandiae* was

Table 6.1 Average rank of species at two sites. (10 = highest, 0 = absent, * = drilled species, † = occasional plant sown many years previously.

RUATANIWHA

(a) Ten highest ranked species in order

Undeveloped 1975		Undeveloped 1978/9		Developed 1978/9	
Festuca novae-zelandiae	(8.5)	*Hieracium praealtum*	(9.3)	*Hieracium praealtum*	(7.0)
Hieracium praealtum	(6.5)	*H. pilosella*	(7.8)	*H. pilosella*	(6.6)
H. pilosella	(4.7)	*Festuca novae-zelandiae*	(6.4)	*Festuca novae-zelandiae*	(5.4)
Aira caryophyllea	(4.7)	*Hypochoeris radicata*	(4.6)	*Rumex acetosella*	(4.0)
Erythranthera pumila	(4.3)	*Pimelea oreophila*	(4.5)	*Erythranthera pumila*	(3.6)
Rumex acetosella	(4.1)	*Erythranthera pumila*	(3.8)	*Trifolium hybridum*	(3.5)
Hypochoeris radicata	(3.9)	*Rumex acetosella*	(3.5)	*T. arvense*	(3.2)
Polytrichum juniperinum	(3.8)	*Cyathodes fraseri*	(3.1)	*Pimelea oreophila*	(2.4)
Vulpia bromoides	(3.1)	*Carex breviculmis*	(2.4)	**T. repens*	(2.3)
**Trifolium repens*	(1.9)	*Polytrichum juniperinum*	(2.0)	*Cyathodes fraseri*	(2.1)

(b) Other species present

Acaena caesiiglauca
Agropyron scabrum
Agrostis tenuis
Anthoxanthum odoratum
Aphanes microcarpa
Bromus mollis
B. tectorum
Bryum sp.
Carex colensoi
C. breviculmis
Carmichaelia petriei
C. monroi
Cassinia fulvida
Cerastium holosteoides
Cotula pectinata
Corallospartium crassicaule
Crepis capillaris
Cyathodes fraseri
Epilobium hectori
Geranium sessiliflorum
Gnaphalium audax
Hieracium lachenalii
Hydrocotyle microphylla
**Lotus corniculatus*
**Lupinus polyphyllus*
Luzula alophylla
Microseris scapigera
Muehlenbeckia axillaris
Oreomyrrhis colensoi
Oxalis corniculata
Pimelea oreophila
P. sericeo-villosa
Poa colensoi
Raoulia australis
R. parkii
R. subsericea
R. tenucaulis
Rosa rubiginosa
Trifolium arvense
T. dubium
T. pratense
Verbascum thapsus
Veronica sp.
Vittadinia australis
Wahlenbergia albomarginata

Table 6.1 (cont.)

SAWDON

(a) Ten highest ranked species in order

Undeveloped 1975		Undeveloped 1978/9		Developed 1978/9	
Hieracium pilosella	(10.0)	*Hieracium pilosella*	(9.6)	**Trifolium repens*	(9.0)
Festuca novae-zelandiae	(7.8)	*Festuca novae-zelandiae*	(6.2)	*Agrostis tenuis*	(8.2)
Anthoxanthum odoratum	(5.1)	*Anthoxanthum odoratum*	(5.1)	*Hieracium pilosella*	(7.0)
Coprosma petriei	(4.9)	*Coprosma petriei*	(4.7)	*Anthoxanthum odoratum*	(4.3)
Agrostis tenuis	(4.7)	*Agrostis tenuis*	(4.6)	**Trifolium hybridum*	(3.7)
Discaria toumatou	(3.7)	*Pyrranthera exigua*	(3.4)	*Rumex acetosella*	(2.3)
†*Trifolium hybridum*	(2.8)	*Discaria toumatou*	(3.3)	**Dactylis glomerata*	(0.6)
Pyrranthera exigua	(2.2)	*Poa colensoi*	(3.0)	**T. pratense*	(0.4)
Aira caryophyllea	(2.0)	*Cyathodes fraseri*	(2.5)	*Festuca novae-zelandiae*	(0.2)
Cyathodes fraseri	(1.1)	**Trifolium repens*	(1.9)	*Discaria toumatou*	(0.1)

(b) Other species present

Aira caryophyllea
Bryum sp.
Carex breviculmis
Celmisia gracilenta
Colobanthus brevisepalus
Cyathodes fraseri
**Dactylis glomerata*
Deyeuxia avenoides
Discaria toumatou
**Festuca arundinacea*
Hieracium praealtum
H. lachenalii
**Holcus lanatus*
Linum catharticum
**Lotus corniculatus*
Luzula rufa
** Medicago sativa*
Prasophyllum colensoi
Polytrichum juniperinum
Raoulia subsericea
Rumex acetosella
Senecio haasti
Stackhousia minima
Wahlenbergia albomarginata

the dominant at the Ruataniwha site. The ranking technique showed that the two *Hieracium* species were the next most common species, even though they had only small cover. As white clover (*Trifolium repens*) was the only sown species to occur in the ten highest ranked it was considered that unimproved and improved paddock results could be combined as indicative of the general vegetation at the start of the trial.

At the Sawdon site, *H. praealtum* was almost absent. *H. piloselLa* was the first ranked species in every quadrat but one of the unimproved paddocks, and most of the improved paddocks. The better moisture and fertility at this site resulted in first summer dominance by the drilled species in the improved paddocks.

Species ordination

At the Ruataniwha site principal factor analysis on the combined data for all paddocks in 1975 showed that nine factors accounted for 60% of the variance from the correlation matrix. The species are plotted in the first three factors which accounted for 50% of the common variance (Fig. 6.1). Spatial proximity on this plotting is indicative of association or similarity of response to some ecological factors. The strength of the relationship between a species and the factor is directly related to the distance from the origin (Gittens 1969). The Ruataniwha site community subdivided into three groups. The first grouping is a tussock association of *Festuca novae-zelandiae*, *Hieracium praealtum* and *Hypochoeris radicata*. The association of

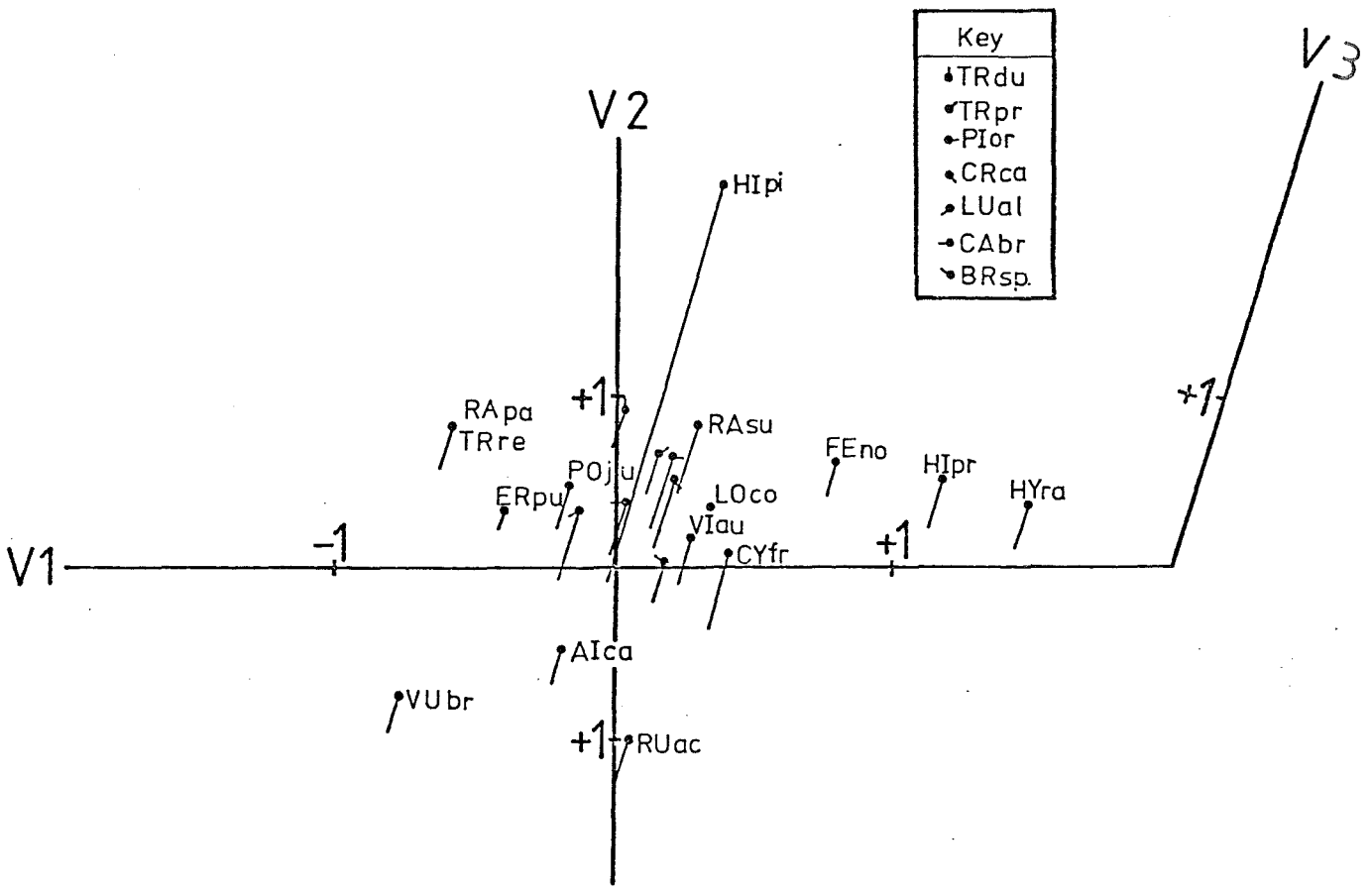


Figure 6.1 Ordination of Ruataniwha species present in more than 5% of the plots on the first three factors of a principal factors solution. The species abbreviated are:

AIca	*Aira caryophyllea*	LUal	*Luzula alophylla*
BRsp	*Bryum* sp	PIor	*Pimelea oreophila*
CAbr	*Carex breviculmis*	POju	*Polytrichum juniperimum*
CRca	*Crepis capillaris*	RApa	*Raoulia parkii*
CYfr	*Cyathodes fraseri*	RAsu	*R. subsericea*
ERpu	*Erythranthera pumila*	RUac	*Rumex acetosella*
FEno	*Festuca novae-zelandiae*	TRdu	*Trifolium dubium*
HIpi	*Hieracium pilosella*	TRpr	*T. pratense*
HIpr	*H. praeltum*	TRre	*T. repens*
HYra	*Hypochoeris radicata*	VIau	*Vittadinia australis*
LOco	*Lotus corniculatus*	VUbr	*Vulpia bromoides*

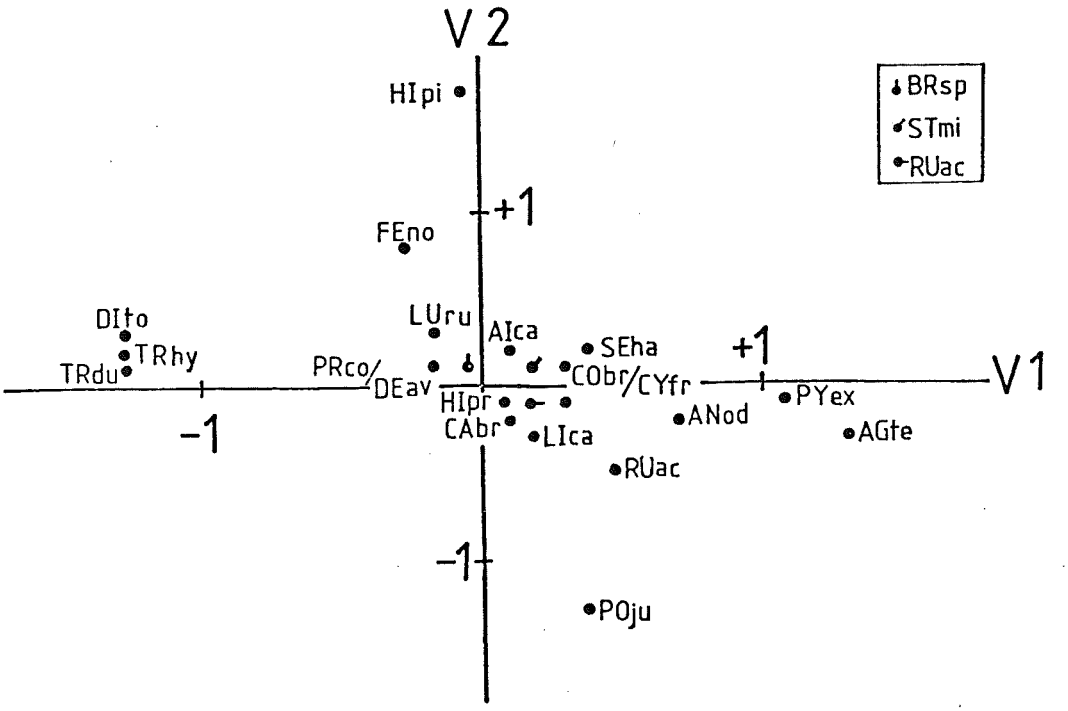


Figure 6.2 Ordination of Sawdon species ranking from unimproved paddocks on 2-axis factor analysis.

AGte	*Agrostis tenuis*	Hipr	*H. praealtum*
AIca	*Aira caryophyllea*	LIca	*Linum Catharticum*
ANod	*Anthoxanthum odoratum*	LUru	*Luzula rufa*
BR	*Bryum* sp.	POju	*Polytrichum juniperinum*
CEbr	*Carex breviculmis*	PRco	*Prasophyllum colensoi*
COBr	*Colobanthus brevisepalus*	PYex	*Pyrranthera exigua*
COpe	*Coprosma petriei*	RAsu	*Raoulia subsericea*
CYfr	*Cyathodes fraseri*	RUac	*Rumex acetosella*
DEav	*Deyeuxia avenoides*	SEha	*Senecio haastii*
DIto	*Discaria toumatou*	STmi	*Stackhousia minima*
FEno	*Festuca novae-zelandiae*	TRhy	*Trifolium hybridum*
HIpi	*Hieracium pilosella*	TRdu	*T. dubium*

H. praealtum and *H. radicata* with the tussock is probably a response to past grazing pressure since these species are highly preferred by sheep in the Mackenzie Country (Hughes 1975, Scott and Maunsell 1974). The second grouping of *Aira caryophyllea, Rumex acetosella* and *Vulpia bromoides* is a characteristic depleted grassland association (Zotov 1939). The species near the origin are the main inter-tussock species plus some of the drilled improvement species. The most conspicuous feature of the ordination is the location of *H. pilosella* in this group and its marked solitary position on the third component. This position indicates a strong negative association with other members of the intertussock community.

The Sawdon unimproved site ordination (Fig. 6.2) is more complex than for Ruataniwha. Ten factors accounted for 65% of the variance from the correlation matrix. The species are plotted on the first two factors which accounted for 40% of the common variance. Groupings and isolated species that could be distinguished with reference to field observations were: a matagouri-clover association (*Discaria toumatou/Trifolium dubium/T. hybridum*); the tussock (*Festuca novae-zelandiae*); the intertussock and rare species (adjacent to the origin); grass mosaics (*Agrostis tenuis, Pyrrhanthera exigua, Anthoxanthum odoratum*); discrete open habitat species (*Raoulia subsericea, Polytrichum juniperinum*); and *Hieracium pilosella*. As before, *H. pilosella* has a markedly solitary position on the ordination. Of importance is the proximity of *H. pilosella* to *Festuca novae-zelandiae*, having regard to the apparent role of *Hieracium pilosella* in displacing the tussocks.

Dominance-diversity analysis

The ten highest ranked species at each site (Table 6.1) were plotted in sequence (Fig. 6.3). Additional species were not included because they individually occupied less than 1.5% of the area sampled and therefore accounted for an insignificant proportion of the total productivity of the communities.

At the Ruataniwha site, the sociological dominant was *Festuca novae-zelandiae* (Table 6.1). The dominance diversity curve for this site (Fig. 6.3a) is curvilinear, indicating a relationship of the type described by the first model (Whittaker 1965) when no single species or group of species dominates the community. In the initial high density *H. pilosella* situation at the Sawdon site, the relationship is essentially linear (Fig. 6.3b), conforming closely to the "niche pre-emptive" model.

In the development series at Ruataniwha a substantial increase in the rank of *H. pilosella* and the establishment of introduced species, particularly the clovers *Trifolium hybridum* and *T. repens*, reduced the diversity of the community and was reflected by a more linear curve (Fig. 6.3c). Development at Sawdon caused the displacement of *H. pilosella* and a co-dominance by *T. repens*, *Agrostis tenuis*, *H. pilosella*, *Anthoxanthum odoratum* and *T. hybridum* which is reflected by the steep slope of the curve (Fig. 6.3d).

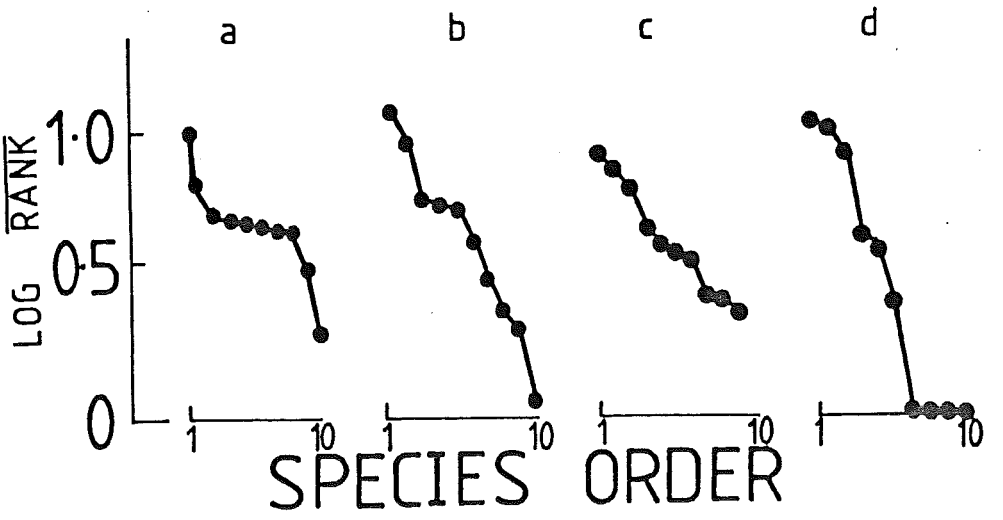


Figure 6.3 Dominance-diversity relationships at Ruataniwha, undeveloped 1975(a), developed 1978/9(b), and Sawdon undeveloped 1975(c), developed 1978(d), for the 10 highest ranked species at each site.

Species time trends

The changes in proportional representation within ranks of *H. pilosella* and *H. praealtum* between 1975/6 and 1978/9 were used to construct a probability transition matrix. An example of this is given in Table 6.2 which shows for instance that given similar trends of the quadrats in which *H. pilosella* initially ranked 1, the probability of still ranking 1 three years later is 8% with the remainder moving down to ranks 2 to 5. Fig. 6.4 shows the initial and third year distribution of *Hieracium* rankings in the various treatments for which transition matrices were derived, together with the predicted distribution in 1981, assuming the same conditions continue.

The Ruataniwha site unimproved paddocks show *H. pilosella* increased in the upper ranks in all paddocks (Fig. 6.4 a-d). *H. praealtum* increased in the summer and winter grazed paddocks and particularly the paddock retired, but remained about the same in the spring grazed paddock.

In the improved series, *H. pilosella* was held at initial proportions in the summer and winter grazed paddock. Increases in the top ranks occurred with spring and rotational grazing. Spring and rotational grazing however held *H. praealtum* to earlier levels while summer and winter grazing worsened the situation.

At the Sawdon site insufficient *H. praealtum* was available to construct matrices for that species. In the unimproved series, *H. pilosella* showed a slight decline in all paddocks as other resident species, mainly

Table 6.2 Example of a probability transition matrix for change in *Hieracium* ranking. Combined developed quadrats from Sawdon site for *H. pilosella*.

		Probability of various ranks 3 years later											
Initial ranking 1975		1	2	3	4	5	6	7	8	9	10	11	12
Most abundant =	1	.08	0	.13	0	0	0	0	0	0	0	0	.08
	2	.21	.02	.37	0	0	0	0	0	0	0	0	.31
	3	.41	.29	.37	0	.25	0	0	0	0	0	0	.38
	4	.23	.33	0	0	0	.50	.50	0	0	0	0	.15
	5	.08	.17	0	.50	.25	0	0	0	0	0	0	.08
Final ranking 1978/9	6	0	.10	0	.50	0	0	0	0	0	0	0	0
	7	0	.50	0	0	0	0	.50	0	0	0	0	0
	8	0	.02	0	0	0	0	0	0	0	0	0	0
	9	0	.02	0	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0	0	0	0
Present =	11	0	0	0	0	0	0	0	0	0	0	0	0
Absent =	12	0	0	.13	0	.50	.50	0	0	0	0	0	0

Table 6.3 Seed production (No. m^{-2}) for *H. pilosella* and *H. praealtum* at Ruataniwha site under different grazing management and development.

	Unimproved		Improved	
Period grazed	*H. pilosella*	*H. praealtum*	*H. pilosella*	*H. praeltum*
Sept. - Dec.	0	0	110	2 300
Jan. - April	3 100	21 200	1 900	4 100

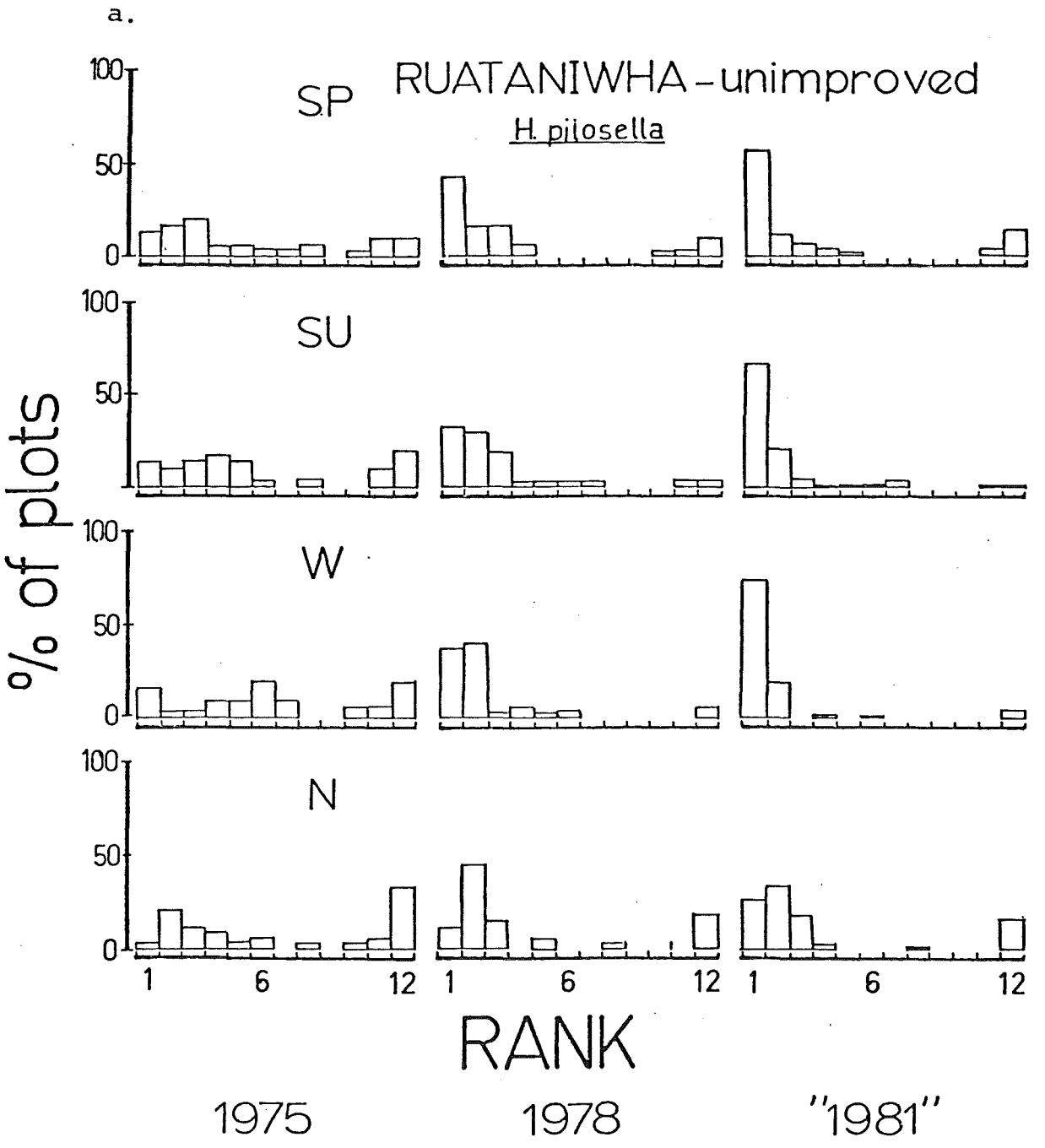
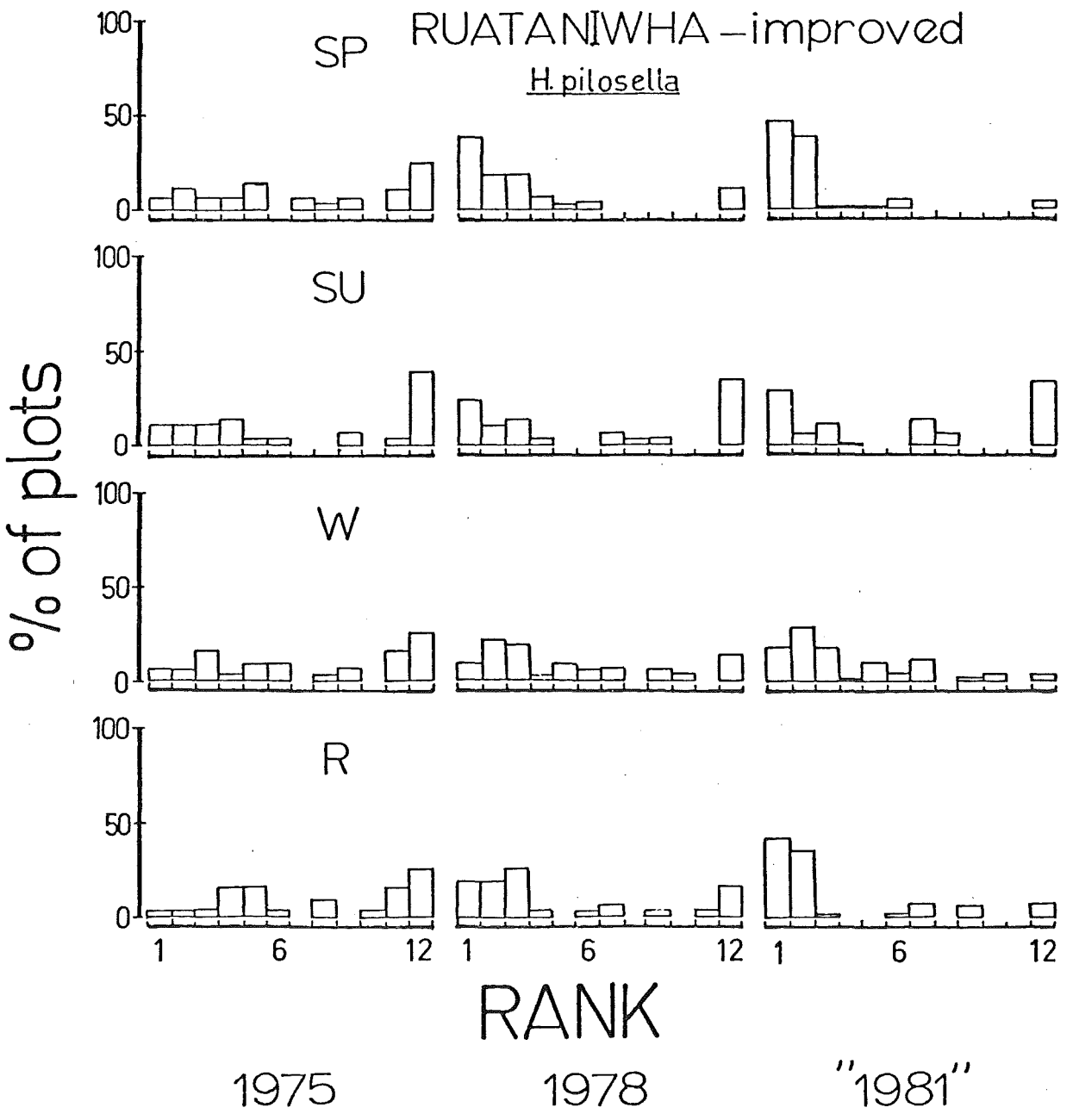
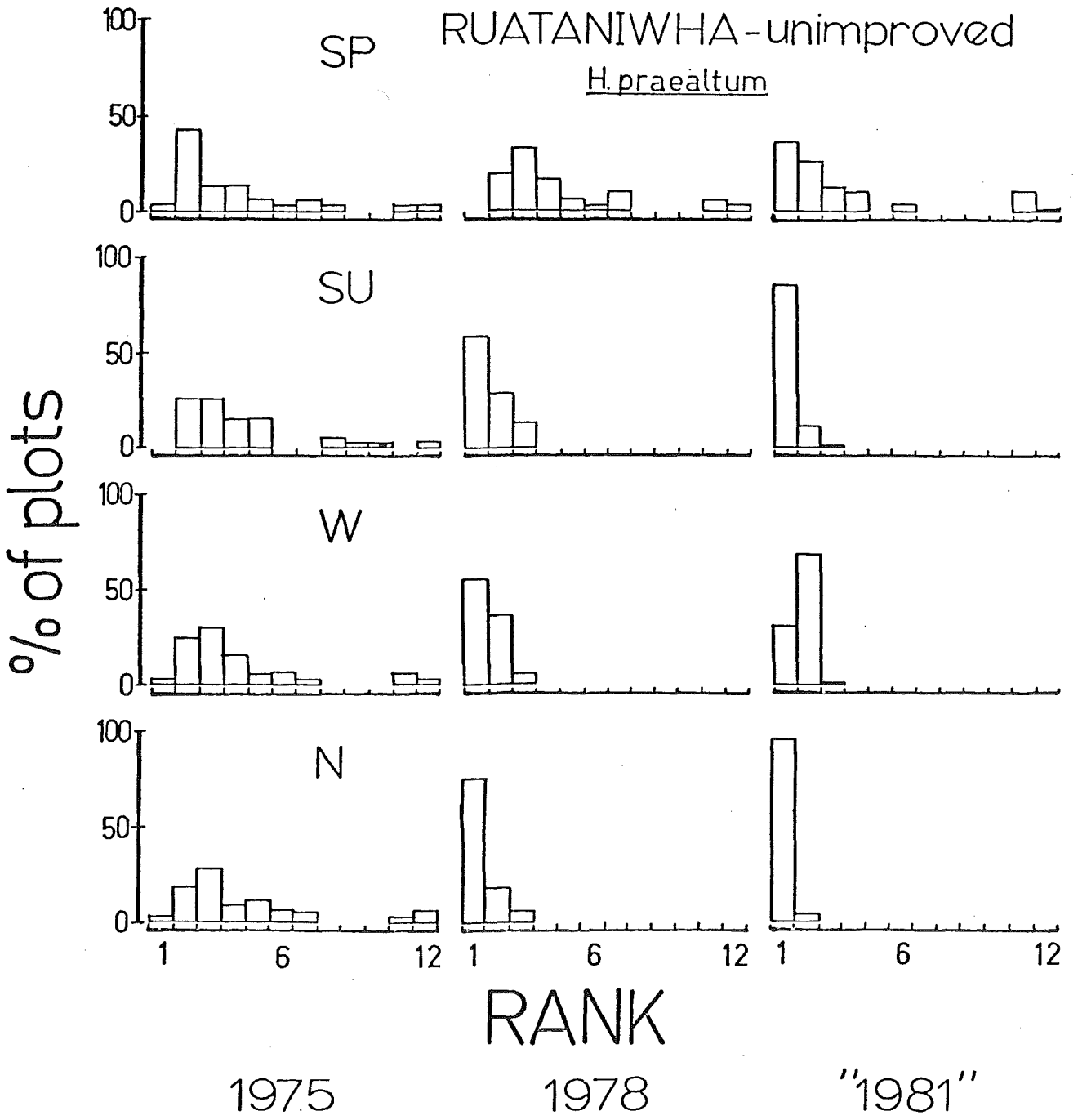


Figure 6.4 a-f: The rank transition of *H. pilosella* and *H. praealtum* (improved) and (unimproved) paddocks with different grazing management.
Rank: 1 = maximum biomas in quadrat, 11 = present, 12 = absent.
Grazing: SP = spring (September-December)
SU = summer (January-April)
W = winter (May- August)
N = nil
R = rotationally grazed.

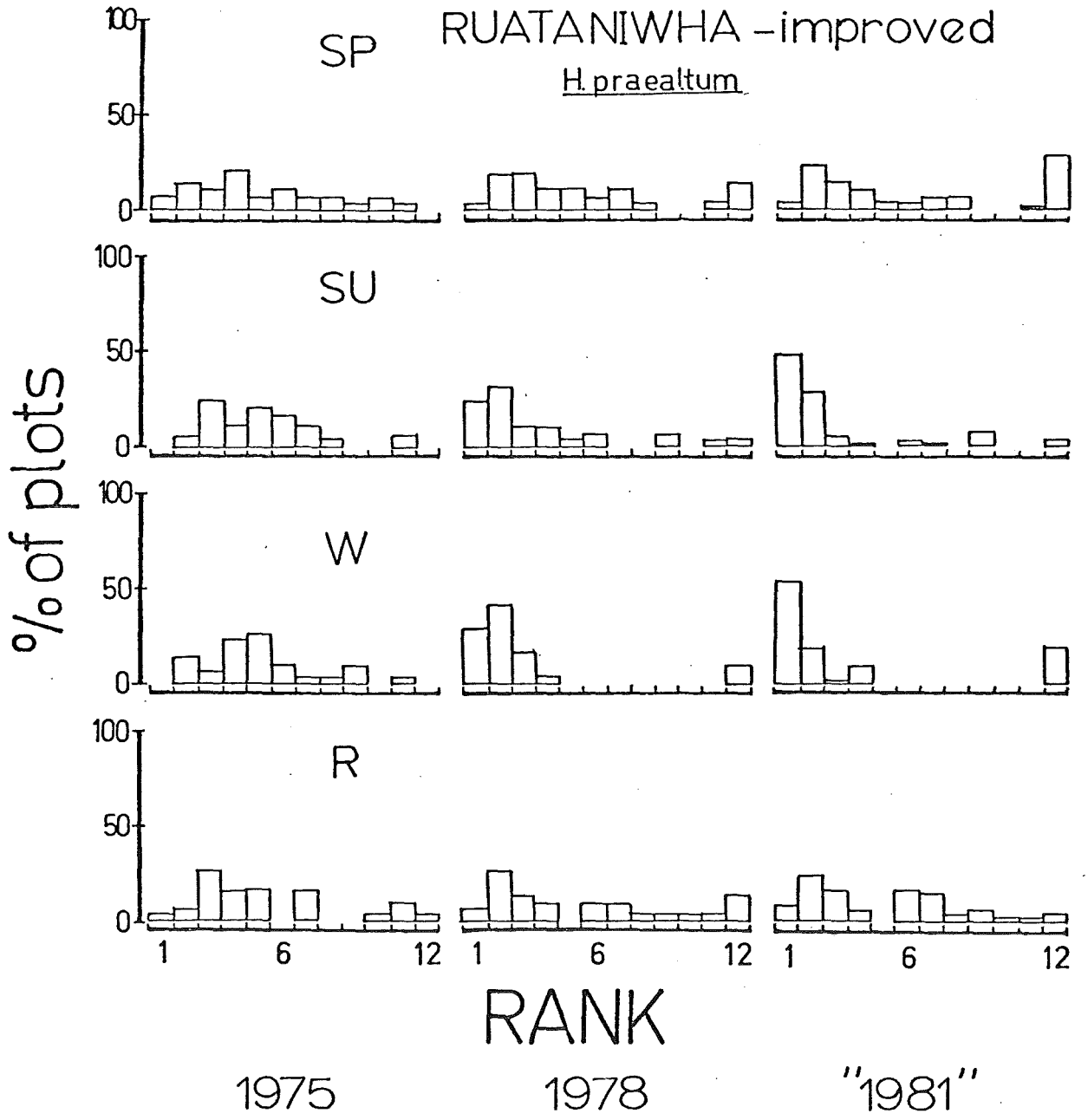
b.


RUATANIWHA – improved
H. pilosella
SP
SU
W
R
100
50
0
% of plots
1
6
12
RANK
1975
1978
"1981"

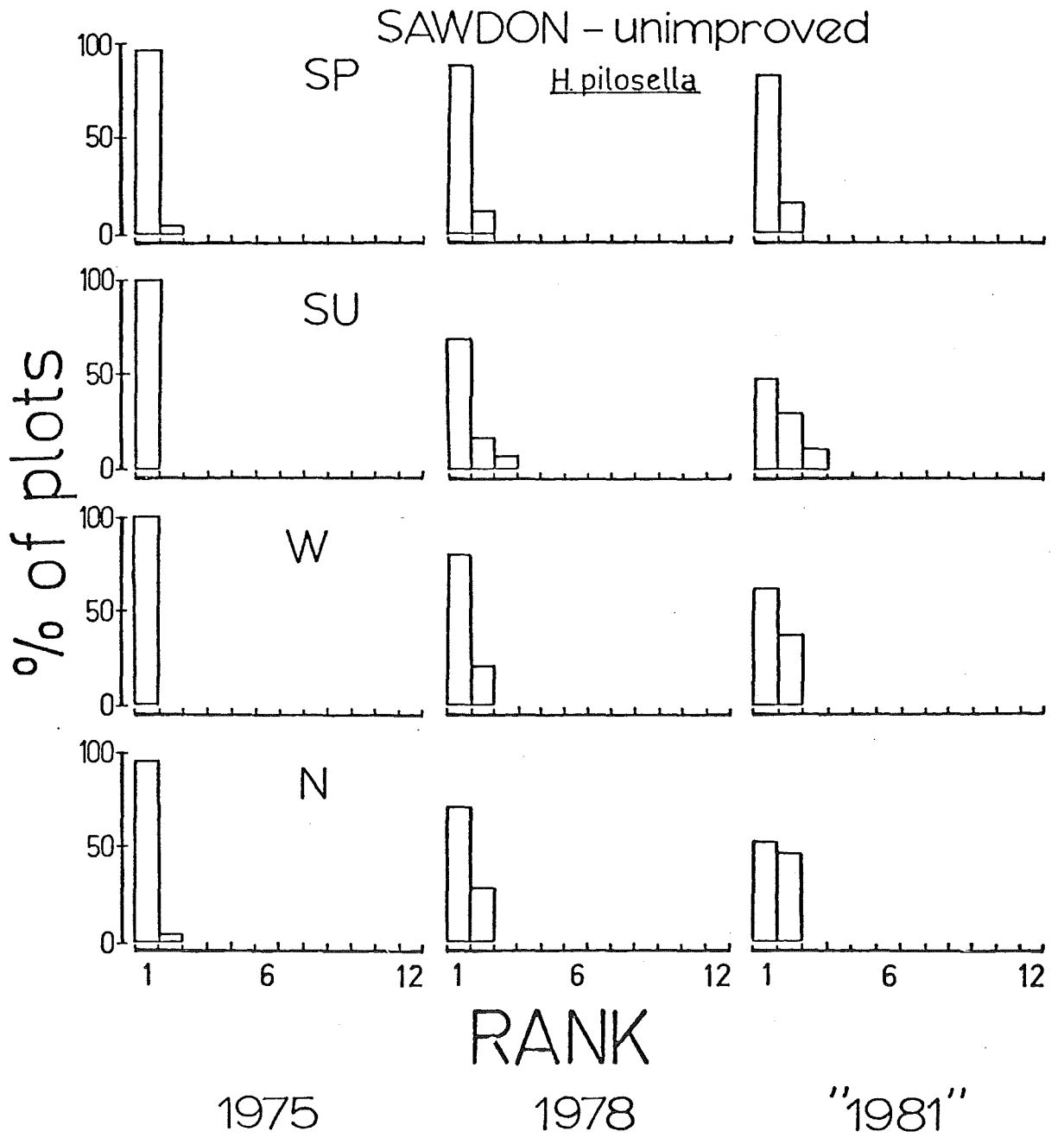
c.


RUATANIWHA-unimproved
H. praealtum
SP
SU
W
N
100
50
0
% of plots
1
6
12
RANK
1975
1978
"1981"

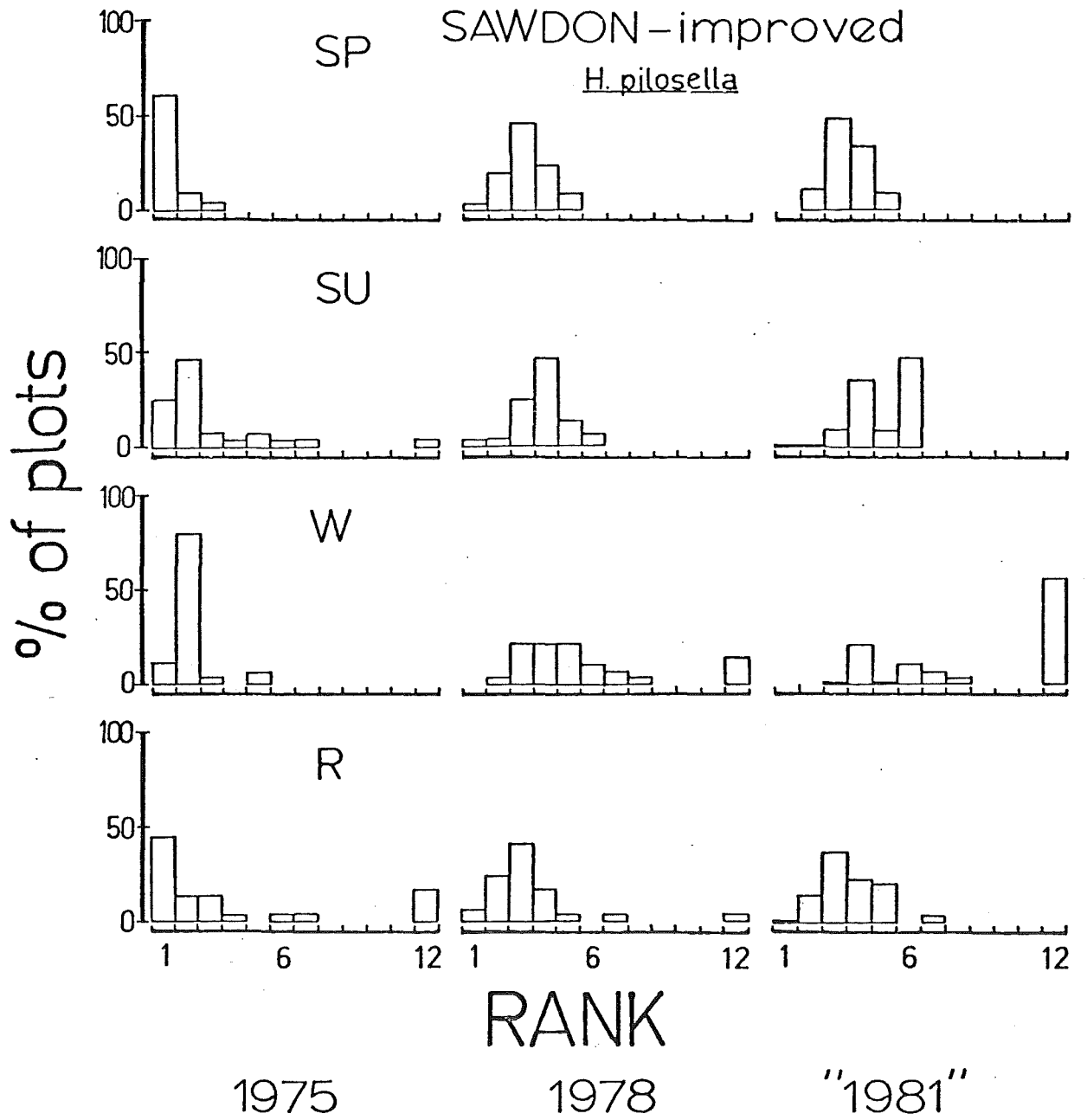
d.


RUATANIWHA - improved
H. praealtum
SP
SU
W
R
100
50
0
% of plots
1
6
12
RANK
1975
1978
"1981"

e.


SAWDON - unimproved
H. pilosella
SP
SU
W
N
100
50
0
% of plots
1
6
12
RANK
1975
1978
"1981"

f.


SAWDON - improved
H. pilosella
SP
SU
W
R
100
50
0
% of plots
1
6
12
RANK
1975
1978
"1981"

browntop (*Agrostis tenuis*), increased (Fig. 6.4 e,f). The improved series showed definite signs of *H. pilosella* control, mainly by the increase of white clover (*T. repens*), and alsike (*T. hybridum*). Rather better control in the winter paddock is attributable to a porina attack at the end of the 1975/6 summer which eradicated most vegetation including *H. pilosella*. Subsequently, alsike re-established from seed.

Seed output

In the 1978/9 season seed output was eliminated by spring grazing in the undeveloped series (Table 6.3). Available forage was lowest in this paddock and inflorescences were grazed as they appeared. Conversely, seed production was highest in the summer grazed paddock in the undeveloped series. Alternative forage in the spring grazed developed paddock enabled both species to produce and disperse seed. The amount of seed dispersal in the summer grazed developed paddock was lower than in the corresponding undeveloped paddock. This difference reflects the effect of competition from the introduced species which overgrew *Hieracium*, since the abundance of both hawkweeds was not as divergent as seed output differences would suggest.

6.4 DISCUSSION

The species ordination showed that unlike *H. praealtum*, *H. pilosella* had very low interspecific sociability at both sites. The combination of vegetative expansion into surrounding vegetation and low sociability support the hypothesis that *H. pilosella* is able to exclude most other

species rather than being an opportunist filling unexploited space. This tendency was also shown by the dominance-diversity analysis.

The trend shown by remeasurement after three years was that the effect of differential development and grazing on the ranking of the two hawkweeds was small. The two species were continuing to increase under all treatments at the Ruataniwha site, though only a few of the drilled species reached agriculturally acceptable levels at that stage. At the Sawdon site *H. pilosella* was tending to decline in the improved and, to a minor degree, in the unimproved treatment.

Detection of these trends was aided by the transition matrix approach, particularly by exaggerating the effect through extrapolation into the next time interval. The limited data from the low number of quadrats per paddock and the short time interval used in constructing the probability transition matrices mean that the prediction of trends must be treated with caution, though confidence is increased by the similarity in trends in the dominance-diversity analysis.

The transition matrix procedure has shown a difference between the species in relation to spring (September-December) grazing. This was the most effective treatment for controlling or decreasing *H. praealtum*, but the least effective for *H. pilosella*.

Since *H. praealtum* was an efficient coloniser of bare ground, the reduction or elimination of seed output by spring grazing (Table 6.3) would check further spread by seed into the large amount of bare ground available at

Ruataniwha. Grazing during this period would also reduce the competitiveness of *H. praealtum*, since besidesbeing an easily grazed species because of its erect growth habit, all leaf growth of overwintering *H. praealtum* plants occurred before the end of this time (Chapter 3).

For similar reasons, spring grazing would increase the competitiveness of *H. pilosella* against taller species since its flat leaves were overtopped to a large degree and their growth was spread over more of the year than that for *H. praealtum*. Although seed output was also prevented by grazing, *H. pilosella* was a poor coloniser of bare ground compared to *H. praealtum* so the elimination of seed would not have much direct effect. However constant removal of inflorescences would promote an increase in vegetative reproduction and the radius of spread (Chapter 3).

CHAPTER 7

OVERVIEW

7.1 CONCLUDING DISCUSSION

Many aspects of the methods used and the results obtained in this study of the ecology of *Hieracium pilosella* and *H. praealtum* have been discussed in previous chapters. The aim of this final discussion is to present an overall summary, synthesising the findings.

Although the mainly sympatric distribution of *H. pilosella* and *H. praealtum* in montane tussock grasslands implies some overlap of their abiotic environmental tolerances, the habitats they occupy and their behaviour in them is different. *H. pilosella* is frequently an invader and clonally expansive species in grazed vegetation. By contrast, *H. praealtum* is an opportunist which colonises disturbed habitats and gaps in the vegetation of lightly grazed and retired grasslands. Subsequent clonal ingress into adjoining vegetation is slight.

The differences between the habitats associated with each species implies that *H. pilosella* and *H. praealtum* occupy different fundamental niches partitioned by at least three gradients

(1) stress,

(2) grazing pressure, and

(3) habitat stability.

A general representation of the modal niches of *H. pilosella* and *H. praealtum* compared with desirable pasture species

characteristics, is presented in Fig. 7.1.

Grime (1979) defined stress as the external constraints which limit dry matter production. The level of stress is the major determinant of plant performance. The most obvious effect of stress is the reduction of the abilities of the more competitive species which favours less competitive species with greater abiotic tolerances. The commonness of *H. pilosella* and *H. praealtum* in low productivity grassland habitats and their rarity in more productive ones indicate that neither species is primarily a competitor strategist, *sensu* Grime (1979). The decreasing growth and reproductive performance of *H. praealtum* relative to *H. pilosella* with increasing stress indicates that *H. pilosella* has greater stress tolerance than *H. praealtum*.

Under grazing, as *H. pilosella* has a very flat-leaved habit and limited morphogenetic response to shade (i.e. overgrowth conditions), it receives much less foliar damage than taller growing species, including *H. praealtum*. Grazing therefore would increase the competitiveness of *H. pilosella* against otherwise superior competitors in several ways. Direct foliar damage eliminates overgrowth and enables the otherwise overtopped plant species to obtain a greater share of the light resource than they would receive beneath foliage. Subsequent rapid foliar regrowth after defoliation is characteristic of its competitors and appears to be attained at the temporary expense of root development (Grime 1979), a condition which would also increase the competitive ability of *H. pilosella*. Although

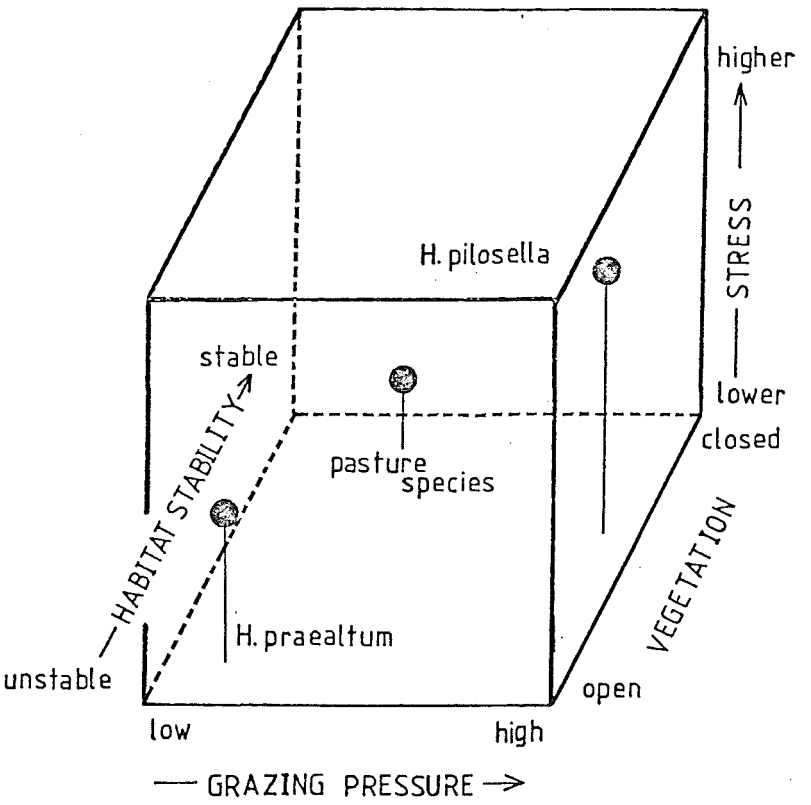


Figure 7.1 A simplified model of the modal niches of *H. pilosella* and *H. praealtum*.

the inflorescences of *H. pilosella* are grazed, their removal causes greater stolon elongation which increases expansiveness into the neighbouring vegetation.

Differences in habitat stability provide an important niche dimension. Although *H. pilosella* colonises bare ground by seed, its performance in this respect is inferior to that of *H. praealtum*. *H. praealtum* seedlings only become established in vegetation gaps. Therefore, in moist habitats where the vegetation is closed, *H. praealtum* is restricted to colonising disturbed microsites.

The environmental and habitat factors which control the performance of *H. pilosella* and *H. praealtum* within the tussock grasslands have been described. The specific characteristics which cause *H. pilosella* to be more troublesome than *H. praealtum* need to be re-emphasized.

Although both species are preferred forage species at low density, the dry matter production of *H. pilosella* is particularly low. Therefore the tendency of *H. pilosella* to form extensive colonies, which eliminate the majority of resident and pasture species through competition and allelopathy, causes a lowering of pasture productivity. By comparison, *H. praealtum* is able to co-exist with other species. The volunteer characteristic of this species in vegetation gaps, together with the moderate dry matter production in undeveloped grasslands, is valuable.

7.2 SUMMARY

1. The objective of the study was to investigate the general biology and ecology of *Hieracium*

pilosella and *H. praealtum* in short tussock (*Festuca novae-zelandiae*) grasslands. The approaches to, and results of, a multifactorial investigation are discussed in the preceding chapters. Eight aspects of the biology of the species are considered:

(a) polymorphism, and chromosomal and genotypic variability,

(b) growth, reproduction and productivity at several montane tussock grassland sites,

(c) ecophysiology of germination, seedling biology and adult shade responses,

(d) soil fertility responses and plant induced soil fertility variation,

(e) allelopathic and competitive interference by *H. pilosella* and *H. praealtum* with resident pasture species,

(f) phytosociological relationships in undeveloped and developed tussock grasslands,

(g) time trends in grasslands with fertiliser input and varied pasture species composition under different grazing management regimes, and

(h) response of the *Hieracium* species to herbicide applications.

2. From 31 populations examined, *H. pilosella* is found to be represented in New Zealand entirely by a pentaploid chromosomal race.

3. *H. pilosella* formed longer stolons and produced fewer seeds than *H. praealtum*. Both species produced similar numbers of daughters and relied heavily (up to 99%) on vegetative reproduction for maintenance and expansion of established populations. The survivorship of *H. pilosella* daughters into autumn was greater than that of *H. praealtum* particularly in the drier regions.
4. Grazing during the flowering period eliminated annual seed production in both species but produced a twofold increase in the length of stolons grown by *H. pilosella*.
5. Considerable variation in the amount of vegetative reproduction (21x) and the length of stolons per plant (144x) occurred between the centre and edges of *H. pilosella* colonies. No such difference was found in *H. praealtum* colonies.
6. The half-life of populations ranged from 0.4 - 13.5 years for *H. pilosella* compared with 0.2 - 1.1 years for *H. praealtum*.
7. More new leaf growth occurred during August - October and mid-January - mid-April in *H. praealtum* than in *H. pilosella*.
8. The net aerial primary production of *H. praealtum* was 2.8x greater than *H. pilosella* at four sites in the Mackenzie Country and ranged from 6 - 135 g m^{-2} for *H. praealtum* to 1 - 50 g m^{-2} for *H. pilosella*.

9. Root shoot ratios were 0.4 - 1.3 for *H. pilosella* and 0.7 - 2.4 for *H. praealtum*.

10. Seed of both species germinated rapidly at warm temperatures without after-ripening. Germination differences which appeared to be related to the preferred habitat of each species were found. The range of suitable temperatures for rapid germination was wider and the optimum higher for *H. praealtum* seed compared with *H. pilosella* seed. *H. praealtum* tolerated more moisture stress during germination than *H. pilosella* but was not superior in this respect to *Trifolium repens*, *T. hybridum* or *Dactylis glomerata*. Light induction was important for germination of most *H. praealtum* seed.

11. *H. praealtum* seed was lighter and had lower endospermic reserves than *H. pilosella* seed. More growth occurred in the shoot compared to the root in *H. praealtum* seedlings than in *H. pilosella* seedlings.

12. *H. pilosella* had a more limited morphological response to shading than *H. praealtum* during both seedling and adult life stages.

13. *H. pilosella* preferred higher soil fertility than *H. praealtum*. *H. pilosella* vegetative reproduction responded to fertilisers. Calcium nitrate increased the number of daughters produced and molybdenum-fortified superphosphate increased the length of stolons.

14. Previous allelopathic research was critically discussed. An approach involving laboratory and field experiments was used. Root abnormality, observable in the field and the laboratory, was used as a definitive marker of allelopathic interference. *H. pilosella* had an allelopathic potential arising in recently dead leaves. The effect was localised at, or near, the litter surface and was mainly associated with a coumarin, umbelliferone (7-hydroxycoumarin). *H. praealtum* was relatively benign. *H. pilosella* inhibited root growth *in vitro* of a range of resident tussock grassland species and reduced the yield of *Dactylis glomerata* and *Trifolium repens* but did not affect the root growth or yield of *T. hybridum*. *Festuca novae-zelandiae* root growth was 50% inhibited by 3×10^{-5} M umbelliferone.

15. Apparent interference of *H. pilosella* with *F. novae-zelandiae* in the field was demonstrated in a glasshouse pot trial. At Cave Stream, the nitrogen and phosphorus composition of leaves was lower in fescue tussock growing in soil shared with *H. pilosella*. The phosphorus differential also occurred in a pot trial.

16. Pasture species used in a replacement series pot trial were: *Trifolium repens*, *T. hybridum*, *Lolium perenne* and *Dactylis glomerata*. *H. praealtum* did not interfere with the yield of the pasture species (except with that of *T. repens* under low

fertility conditions). *H. pilosella* exceeded expected yields when grown with *D. glomerata*, *L. perenne* and *T. repens* under conditions of low water availability and with *T. repens* and *T. hybridum* at low fertility. *T. hybridum* suppressed *H. pilosella* under combined conditions of higher soil fertility and favourable moisture availability.

17. *H. pilosella* had a very low interspecific sociability compared to *H. prealtum* or other resident tussock grassland species.

18. Control of *H. pilosella* on one of the better soils at a moist site (Sawdon Station, Chapter 3) was achieved to a large extent with an input of fertiliser in association with drilling of pasture species, together with suitable grazing management. *H. praealtum* was rare before and after development at this site. On shallow soil at a drier site (Ruataniwha Station, Chapter 3) no reduction in either *H. pilosella* or *H. praealtum* was achieved by fertiliser input or drilling of pasture species over the same period, although alternative forage was gained which increased the carrying capacity. Spring (September to December) grazing checked *H. praealtum* but increased *H. pilosella*.

19. Dowco 290 + 2,4-D esters gave a high degree of control of *H. pilosella* at 400 + 1 000 g ha^{-1} compared with previously recommended herbicides. Resident grasses,

mainly *Agrostis tenuis* and *Anthoxanthum odoratum*, and alsike clover (*Trifolium hybridum*) were adversely affected immediately after spraying but recovered well. The use of herbicides is not recommended except as a prelude to development of *H. pilosella* dominant communities on relatively deep, fertile soils with sufficient moisture to prevent soil loss through wind erosion. Only under these circumstances is it possible to re-establish vegetation cover rapidly.

20. While *H. praealtum* is agronomically valuable under low soil fertility conditions in tussock country, *H. pilosella* lowers dry matter production and its presence in short tussock grasslands is deleterious to their carrying capacity.

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Allan, H.H. (1920) A note on weeds. The Magazine of the Agricultural and Pastoral Association, 1, 39-40.

Allan, H.H. (1940) A handbook of the naturalised flora of New Zealand. DSIR Research Bulletin 83.

Allen, S., H.M. Grimshaw, J.A. Parkinson and C. Quarmby (1974) Chemical Analysis of Ecological Materials. Blackwell Scientific Publications, Oxford.

Anderberg, M.R. (1973) Cluster Analysis for Applications. Academic Press, New York.

Anonymous (1976) *Hieracium* - good or bad? Tussock Grasslands and Mountain Lands Institute Review, 32, 48-54.

Audus, L.T. (1972) Plant growth substances. In Chemistry and Physiology. N. Polunin (ed.), Leonard Hill, London.

Avers, C.J. and R.H. Goodwin (1956) Studies on roots IV. Effects of coumarin and scopoletin on the standard root growth pattern of *Phleum pretense*. American Journal of Botany, 43, 612-620.

Baker, H.G. (1974) The Evolution of Weeds. Annual Review of Ecology and Systemmatics, 5, 1-24.

Barker, A.P. (1953) An ecological study of tussock grassland Hunters Hills, South Canterbury. DSIR Research Bulletin 107.

Bate-Smith, E.C., P.D. Sell and C. West (1968) Chemistry and taxonomy of *Hieracium* L. and *Pilosella* Hill. Phytochemistry, 7, 1165-69.

Becker, Y., and L. Guyot (1951) Sur les toxines racinaires des sols incults. Compte Rendu Hebdomadaire des Séances de l' Academie des Sciences, 232, 105-7.

Bingham, S.W. (1965) Hawkweed control with turf herbicides. Proceedings of the 19th Annual Meeting, Northeastern Weed Control Conference, 486-9.

Bishop, G.F., A.J. Davy and R.L. Jeffries (1978). Demography of *Hieracium pilosella* in a Breck grassland. Journal of Ecology, 66, 615-29.

Bollard, E.G. (1966) A comparative study of the ability of organic nitrogenous compounds to serve as sole sources of nitrogen for the growth of plants. Plant and Soil, 25, 153-166.

Bremner, J. (1965) Nitrogen availability indexes. In Methods of Soil Analysis. C.A. Black, D.D. Evans, J.L. White, L.E. Emsmingo, and F.E. Clark, (eds.) American Society of Agronomy, Madison.

Cavers, P.B. and Harper, J.L. (1966) Germination polymorphism in *Rumex crispus* and *Rumex obtusifolius*. Journal of Ecology, 54, 307-82.

Cavers, P.B. and Harper, J.L. (1967) The comparative biology of closely related species living in the same area. IV *Rumex* : the nature of adaptation to a sea-shore habitat. Ibid, 55, 73-82.

Chou, Chang-Hung and C.H. Muller (1972) Allelopathic mechanisms of *Arctostaphylos glandulosa* var. zacaensis. American Midland Naturalist, 88, 324-47.

Clausen, J., D.D. Keck, and W.H. Hiessy (1940) Experimental Studies on the Nature of the Species. I.The effect of varied environments on Western North American plants. Publications of the Carnigie Institution, 520.

Cockayne, L. (1967) New Zealand Plants and Their Story. 4th edition. Govt. Printer, Wellington.

Connor, H.E. (1964) Tussock grassland communities in the Mackenzie Country, South Canterbury, New Zealand. N.Z. Journal of Botany, 2, 325-51.

Dagnelie, P. (1973) L´ Analyse factorielle. In Ordination and Classification of Communities, edited by R.H. Whittaker, and Dr. W. Junk, The Hague.

D´Amato, F. and M.G. D´Amato-Avanzi (1954) The chromosome - breaking effect of coumarin derivatives in the *Allium* test. Caryolgia, 6, 134-50.

Dawes, D.S. and N.C. Maravolo (1973) Isolation and characteristics of a possible allelopathic factor supporting the dominent role of *Hieracium aurantiacum* in the bracken-grasslands of northern Wisconsin. Wisconsin Academy of Sciences, Arts and Letters, 61, 235-61.

Debussche, M., M. Godron, J. Lepart and F. Romane (1977) An account of the use of transition matrix. Agro-Ecosystems, 3, 81-92.

Delcourt, E. (1972) Contribution à l' étude cytotaxinomique de *Hieracium pilosella* L. Bulletin Societie Botanique France, 119,287-302.

Dobinson, J. (1976) The Life Histories and Reproductive Strategies of Three Species of *Rumex* L. Ph.D. Thesis, University of Canterbury, Christchurch.

Dowling, P.M., R.J. Clements and J.R. McWilliam (1971) Establishment and survival of a pasture species from seeds sown on the soil surface. Australian Journal of Agricultural Research, 22, 61-74.

Duffy, E., M.G. Morris, J. Sheail, L.K. Ward, D.A. Wells and T.C.E. Wells (1974) Grassland Ecology and Wildlife Management. Chapman and Hall, London.

Dunbar, G.A. (1977) Another *Hieracium*. Tussock Grasslands and Mountain Lands Institute Review, 35, 68.

Duquénois, P., E. Greib and M. Haag (1956) Dévelopment et de activité l' *Hieracium Pilosella* L au cours de sa végétation. Bulletin Societie Botanique France, 103, 426-29.

Ellenberg, H. (1974) Zeigerwerte der Gefä Bpflanzen Miteleuropas. Scripta Geobotanica, 9, 1-97.

Enright, N. and J. Ogden (1979) Application of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. Australian Journal of Ecology, 4, 3-23.

Freese, F. (1962) Elementary forest sampling. U.S. Department of Agriculture Handbook 232.

Gadella, T.W.J. (1972) Biosystematic Studies in *Hieracium pilosella* L. and some related species of the subgenus *Pilosella*. Botaniska Notiser, 125, 361-9.

Garb, S. (1961) Differential growth-inhibiters produced by plants. Botanical Review (Lancaster), 26, 422-43.

Gittens, R. (1969) The application of ordination techniques. In Ecological Aspects of the Mineral Nutrition of Plants. Blackwell, Oxford.

Glass, A.D.M. (1973) Influence of phenolic acids on ion uptake. I. Inhibition of phosphorus uptake. Plant Physiology Lancaster, 51, 1037-41.

Gliessman, S.R. and C.H. Muller (1978) The allelopathic mechanisma of dominance in bracken (*Pteridium aquilinum*) in Southern California. Journal of

Goodall, D.W. (1970) Statistical Plant Ecology. Annual Review of Ecology and Systematics, 1, 99-124.

Grace, N.D. and D. Scott (1974) Diet and mineral nutrition of sheet on undeveloped and developed tussock grassland. I. The macro- and micro-element composition of blood plasma and herbage. N.Z. Journal of Agricultural Research, 17, 165-75.

Gradwell, M.W. (1955) Soil frost studies at a high country station II. N.Z. Journal of Science and Technology, 37B, 267-75.

Grime, J.P. (1965) Comparative experiments as a key to the ecology of flowering plants. Ecology, 46, 513-5.

Grime, J.P. (1979) Plant Strategies and Vegetation Processes. John Wiley, Chichester.

Grime, J.P. and B.C. Jarvis (1975) Shade avoidance and shade tolerance in flowering plants. II. Effects of light on the germination of species of contrasted ecology in Light as an Ecological Factor : II. Eds. G.C. Evans, R. Bainbridge and O. Rackham. Blackwell, Oxford.

Guenzi, W.D. and T.M. McCalla (1966) Phytotoxic substances extracted from soil. Soil Science Society of America Proceedings, 30, 214-6.

Guyot, A.L. (1956) Les microassociations végétales au sein dur brometum erecti. Vegetatio, 7, 321-54.

Guyot, A.L., Y. Becker, M. Massenot, and J. Montigut (1951) Les excrétions racinaeres toxiques chez lez végétaux. Bulletin technique d'Information des Ingénieurs des Services Agricoles, 59, 346-59.

Harborne, J.B. (1973) Phytochemical Methods. Chapman and Hall, London.

Harborne, J.B. (1977) Biochemical interaction between higher plants. In Introduction to Ecological Biochemistry. J.B. Harborne (ed.) Academic Aess. London.

Harper, J.L. (1977) The population biology of plants. Academic Press, London.

Harris, R.J. (1975) A Primer of Multivariate Statistics. Academic Press, New York.

Harris, W. (1968) The Variation and Ecology of *Rumex acetosella* L. Ph.D. Thesis, University of Canterbury.

Hay, J.R. and G.J. Ouellette (1959) The role of fertiliser and 2,4-D in the control of pasture weeds. Canadian Journal of Plant Science, 39, 278-83.

Healy, A.J. (1969) The adventive flora in Canterbury. In The Natural History of Canterbury, edited by G.A. Knox. A.H. and A.W. Reed, Wellington.

Healy, A.J. (1976) Identification of Weeds and Clovers. Editorial Services, Wellington.

Heywood, V.H. (1967) Plant Taxonomy. Edward Arnold, London.

Howard, W.E. (1958) The Rabbit Problem in New Zealand DSIR Information, Series 16.

Hughes, J.G. (1975) What sheet eat on developed and undeveloped high country. Tussock Grasslands and Mountain Lands Institute Review, 31, 20-30.

Hunt, R. (1978) Plant Growth Analysis. Edward Arnold, London.

Johnson, C.D. and A.G. Thomas (1978) Recruitment and survival of seedlings of a perennial *Hieracium* species in a patchy environment. Canadian Journal of Botany, 56, 572-80.

Kaminsky, R. and W.H. Muller (1977) The extraction of soil phytoxins using a neutral EDTA solution. Soil Science, 124, 205-10.

Kerr, C.J. (1950) The Pastoral Areas of the South Canterbury District. Pts. I and II. South Canterbury Catchment Board, Timaru.

Knox, G.A. (1969) The Natural History of Canterbury. A.H. and A.W. Reed, Wellington.

Kranz, E. and F. Jacob (1977a) Zur mineralstoff-konkurrenz zwischen *Linum* and *Camelina* I. Aufnahme von ^{35}S - Sulfat. Flora, 166, 491-503.

Kranz, E. and F. Jacob (1977b) Zur mineralstoff-konkurrenz zwischen *Linum* and *Camelina* II. Aufnahme von ^{32}P - phosphat und ^{86}Rhubidium. Ibid, 166, 505-516.

Lagerwerff, J.V., G. Ogata and H.E. Eagle (1961) Control of osmotic pressure of culture solutions with polyethylene glycol. Science, 133, 1486-7.

Lawler, D.W. (1970) Absorption of polyethylene glycols by plants and their effects on plant growth. New Phytologist, 69, 501-13.

Mahanty, H.K. (1970) A cytological study of the *Zingiberales* with special reference to their taxonomy. International Journal of Cytology, 35, 13-49.

Makepeace, W. (1976) Allelopathy of mouse-ear hawkweed. Proceedings of the 29th N.Z. Weed and Pest Control Conference, 106-9.

Mannetje, L. and Haydock, K.P. (1963) The dry-weight rank method for the botanical analysis of pasture. British Grasslands Society Journal, 18, 268-75.

Mark, A.F. (1969) The environment and growth rate of narrow-leaved snow tussock, *Chionochloa rigida* in Otago. N.Z. Journal of Botany, 4, 392-7.

Matthews, L.J. (1975) Weed Control by Chemical Methods. Government Printer, Wellington.

Meylaender, M. M. Reuther and P. Duquénois (1968) La *piloselle* cultive : variations morphologiques et chemiques sous l'influence des engrais. Plantes Medicinales et Phytotherapie, 2, 13-25.

Molisch, H. (1937) Der Einfluss einer Pflanze auf die andere - Allelopathie. Fisher, Jena.

Molloy, B.P.J. (1964) Sweet brier, a vigorous woody weed in South Island tussock grassland. New Zealand Journal of Agriculture, 109, 105-18.

Mott, J.J. (1974) Factors affecting seed germination in three annual species from an arid region of Western Australia. Journal of Ecology, 62, 699-709.

Moore, D.R.E. and J.S. Waid (1971) The influence of washings of living roots on nitrification. Soil Biology and Biochemistry, 3, 69-83.

Moore, L.B. (1955) The plants of tussock grassland. Proceedings N.Z. Ecological Society, 3, 7-8.

Moore, L.B. (1976) The Changing Vegetation of Molesworth Station, New Zealand, 1944 to 1971. DSIR Bulletin 217.

Muller, C.H. (1966) The role of chemical inhibition (allelopathy) in vegetational composition. Bulletin of the Torrey Botanical Club, 93, 332-51.

Muller, C.H. (1969) Allelopathy as a factor in ecological process. Vegetatio, 18, 348-57.

Muller, C.H. (1974) Allelopathy in the environmental complex. In Handbook of Vegetation Science V. Strain, B.R. and W.D. Billinger (eds.). Junk, The Hague.

Muller, C.H. and C.H. Chou (1972) Phytoxins: an ecological phase in phytochemistry. In Phytochemical Ecology. J. B. Harborne (ed.) Academic Press, London.

McCalla, T.M. (1971) Studies on Phytotoxic substances from soil microorganisma and crop residues at Lincoln, Nebraska. In Biochemical Interaction Among Plants. Environmental Physiology Subcommittee (ed.). National Academy of Sciences, Washington.

Macfarlane, M.J. (1980) Allelopathic effects of White Clover (*Trifolium repens* L.) on Pasture Species in the High Country Environments. M.Sc. Thesis, Lincoln College, Canterbury.

McPherson, J.K. Chang-Hung Chow and C.H. Muller (1971) Allelopathic constituents of the chaparral shrub *Adenostoma fasciculatum*. Phytochemistry 10, 2925-33.

McWilliam, J.R., R.J. Clements and P.M. Dowling (1970) Some factors influencing the germination and early seedling development of pasture plants. Australian Journal of Agricultural Research, 21, 19-32.

Neal, J.L. (1969) Inhibition of nitri-flying bacteria by grass and forb root extracts. Canadian Journal of Microbiology, 15, 633-5.

Newman, E.I. and M.H. Miller (1977) Allelopathy among some British grassland species. II. Influence of root exudates on phosphorus uptake. Journal of Ecology, 65, 399-411.

N.Z. Meteorological Service (1973) Summaries of Climatological Observations to 1970. New Zealand Meteorological Service, Wellington.

N.Z. Soil Bureau (1968) General Survey of the Soils of South Island, New Zealand. DSIR Soil Bureau Bulletin 27, Wellington.

N.Z. Weed and Pest Control Society (1969). Standard Common Names for Weeds in New Zealand. Editorial Services, Wellington.

Nie, N.E., Hull, C.H. Jenkins, J.G., Streinbrenner, K., and D.H. Bent (1975) Statistical Package for the Social Sciences, 2nd edition. K.J. Boman and M. Cahill (eds.), McGraw-Hill, New York.

O'Connor, K.F. (1976) An Introduction to the Waitaki. New Zealand Man and the Biosphere, Report 1.

Ondok, J.P. (1971) Indirect estimation of primary values used in growth analysis in Plant Photosynthetic Production. Sestâk, Z., J. Catsky, and P.G. Jarvis (eds.), Junk, The Hague.

Payton, I.J. and D.J. Brasch (1978) Growth and nonstructural carbohydrate reserves in *Chionochloa rigida* nd *C. macra*, in their short-term response to fire. N.Z. Journal of Botany, 16, 435-60.

Panebianco, R. and R.W. Willemsen (1976) Seed germination of *Hieracium pratense*, a successional perennial. Botanical Gazette, 137, 255-61.

Patrick, Z.A. (1971) Phytotoxic substances associated with the decomposition in soil of plant residues. Soil Science, 3, 13-18.

Peterson, R.L. (1979) Root buds in *Hieracium florentinum:* effects of nitrogen and observations on bud growth. Botanical Gazette, 140, 407-13.

Pugsley, H.W. (1948) A rpodromus of the British *Hieracia.* Journal of the Linnean Society of London, 54, 1-356.

Raju, M.V.S., R.T. Coupland and T.A. Stevens (1966) On the occurrence of root buds on perrenial plants in Saskatchewan. Canadian Journal of Botany, 44, 33-37.

Reader, R.J. (1978) Structural changes in a *Hieracium floribundum* (Compositae) population associated with the process of patch formation. Canadian Journal of Botany, 56, 1-9.

Ribéreau-Gayon, P. (1968) Plant Phenolics. Oliver and Boyd, Edinburgh.

Rice, E.L. (1974) Allelopathy. Academic Press, New York.

Rice, E.L. (1979) Allelopathy - an update. Botanical Review 45, 17-109.

Salisbury, E.J. (1942) The Reproductive Capacity of Plants. G. Bell and Sons, London.

Sampford, M.R. (1962) An Introduction to Sampling Theory. Oliver and Boyd, Edinburgh.

Scott, D. (1961) Influence of tussock grasses on zonation of accompanying smaller species. New Zealand Journal of Science, 4, 116-22.

Scott, D. (1962) Temperature and light micro-climate within a tall tussock community. N.Z. Journal of Agricultural Research, 5, 179-82.

Scott, D. (1965) A height frequency method for sampling tussock and shrub vegetation. N.Z. Journal of Botany, 3, 253-60.

Scott, D. (1969) Relationship between some statistical methods. Proceedings N.Z. Ecological Society, 16, 58-64.

Scott, D. (1975) Allelopathic interaction of resident tussock grassland species on germination of oversown seed. New Zealand Journal of Experimental Agriculture, 3, 135-41.

Scott, D. (1977a) Plant ecology above timberline on Mt. Ruapehu, North Island, New Zealand. I. Site factors and plant frequency. N.Z. Journal of Botany, 15, 255-94.

Scott, D. (1977b) Plant ecology above timberline on Mt. Ruapehu, North Island, New Zealand. II. Climate and monthly growth of five species. Ibid, 15, 295-310.

Scott, D. (1977c) Plant ecology above timberline on Mt. Ruapehu, North Island, New Zealand. III. Discussion of approach, results, and implications. Ibid, 15, 311-22.

Scott, D. (1979) Potential pasture production in hill and high country. In Hill and High Country Seminar. Tussock Grasslands and Mountain Lands Institute Special Publication No. 16.

Scott, D. and L.A. Maunsell (1974) Diet and mineral nutrition of sheep on undeveloped and developed tussock grassland. II. Vegetation composition and availability. New Zealand Journal of Agricultural Research, 17,

Scott, D., and A.R. Wallace (1978) Effect of ground cover and tussock proximity on legume establishment. N.Z. Journal of Agricultural Research, 21, 93-105.

Sell, P.D. and C. West (1976) *Hieracium*. In Flora Europaea V.4. T.G. Tutin, V.H. Heywood, N.A. Burgess, D.M. Moore, D.H. Valentine, S.M. Walters, and D.A. Webb (eds.). Cambridge University Press, Cambridge.

Simpson, M.J.A. and L.B. Moore (1955) Seedling studies in fescue-tussock grassland. I. Some effects of shading, cultivation and frost. N.Z. Journal of Science and Technology, 37A, 93-9.

Slavik, B (1974) Methods of Studying Plant Water Relations, Academia, Prague.

Sokal, R.R. and F.J. Rohlf (1969) Biometry. Freeman and Company, San Francisco.

Snedecor, G.W. and Cochran, W.G. (1969) Statistical Methods. 6th edition. Iowa University Press, Ames.

Stevens, E.J. and Hughes, J.G. (1973) Distribution of sweet briar, broom and ragwort on Molesworth Station. Tussock Grassland and Mountain Lands Institute Special Publication 9.

Stergios, B.G. (1976) Achene production, dispersal, seed germination and seedling establishment of *Hieracium aurantiacum* in an abandoned field community. Canadian Journal of Botany, 54, 1189-97.

Streibig, J.C. (1979) Numerical methods illustrating the phytosociology of crops in relation to weed flora. Journal of Applied Scology, 16, 577-87.

Thomas, A.G. (1972) Autecological studies of *Hieracium* in Wellington County, Ontario. Ph.D. Thesis, University of Guelph, Guelph.

Thomas, A.G. and H.M. Dale (1974) Zonation and regulation of old pasture populations of *Hieracium floribundum*. Canadian Journal of Botany, 52, 1451-58.

Thomas, A.G. and H.M. Dale (1975) The role of seed reproduction in the dynamics of established populations of *Hieracium floribundum* and a comparison with that of vegetative reproduction. Canadian Journal of Botany, 53, 3022-31.

Thomas, A.G. and H.M. Dale (1976) Cohabitation of three *Hieracium* species in relation to the spatial heterogeneity in an old pasture. Ibid, 54, 2517-29.

Thompson, P.A. (1973) Seed germination in relation to ecological and geographical distribution. In Taxonomy and Ecology. V.H. Heywood (ed.) Academic Press, London.

Tietema, T. (1979) The ecophysiology of the sand sedge (*Carex arenaria*): the response to local mineral sources p638. In Ecological Processes in Coastal Environments. Jeffries, R.L. and A.J. Davey (eds.) Blackwell Scientific Publications, Oxford.

Tietema, T., and J. Vroman (1978) Ecophysiology of the sand sedge *Carex arenaria* L. I. Growth and dry matter distribution. Acta Botanica Neerlandica, 27, 161-73.

Trenbath, B.R. (1978) Models and the interpretation of mixture experiments. In Plant Relations in Pastures. J.R. Wilson (ed.). CSIRO, Melbourne.

Turesson, G. and B. Turesson (1960) Experimental studies in *Hieracium pilosella* L. I. Reproduction, chromosome number and distribution. Hereditas, 46, 717-36.

Van Hulst, R. (1979) On the dynamics of vegetation: Markov chains as models of succession. Vegetatio, 40, 3-14.

Vander Kloet, S.P. (1978) Biogeography of *Hieracium pilosella* L. In North America with special reference to Nova Scotia. Proceedings of Nova Scotia Institute of Science, 28, 127-34.

Voss, G. and M.W. Böhlke (1978) The status of certain hawkweeds (*Hieracium* subgenus *Pilosella*) in Michigan. Michigan Botanist, 17, 35-47.

Walker, J.R.L. (1975) The Biology of Plant Phenolics. Edward Arnold, London.

Wang, T.S.C., S.Y. Cheng and H. Tung (1967) Extraction and analysis of soil organic acids. Soil Science 103, 360-7.

Watt, A.S. (1947) Pattern and process in the plant community. Journal of Ecology, 35, 1-22.

Watt, A.S. (1962) The effect of excluding rabbits from grassland A (xerobrometum) in Breckland, 1936-60. Journal of Ecology, 50, 181-98.

Wells, P.V. (1964) Antibiosis as a Factor in Vegetation Process. Science, 144, 889-90.

Whittaker, R.H. (1965) Dominance and diversity in land plant communities. Science. 147, 250-60.

Whittaker, R.H. (1970) Biochemical ecology of higher plants. In Chemical Ecology, E. Sondheimer and J.B. Simeone (eds.). Academic Press, New York.

Whittaker, R.H. and P.P. Feeny (1971) Allelochemics: Chemical interactions between species. Science, 171, 757-770.

Widera, M. (1978) Competition between *Hieracium pilosella* L. and *Festuca Rubra* L. under natural conditions. Ekologia Polska 26, 359-90.

Witt, C.T. de (1960) On Competition. Verslagen Landbouwkundige Onderzoekingen, 66, 1-82.

Yeung, E.C. and R.L. Peterson (1972) Studies on the rosette plant *Hieracium floribundum*. I. Observations related to flowering and auxillary bud development. Canadian Journal of Botany, 50, 73-8.

Zotov, V.D. (1939) Survey of the tussock-grasslands of the South Island, New Zealand. New Zealand Journal Science and Technology, 20, 212-244.

APPENDIX A

Temperature and precipitation summaries from 3 Upper Waitaki N.Z. Meteorological Service Climatologic Stations for the period July 1978 - April 1979. Compiled from New Zealand Meteorological Service Extracts, New Zealand Gazette, September 1978 (81) - July 1979 (62).

	Temperature						Precipitation	
	Average Maximum	Average Minimum	Average	Deviation from Normal	Extreme Maximum	Extreme Minimum	Total mm	Deviation from Normal
July 1978								
The Hermitage	6.3	-0.8	2.8	+0.9	10.9	-4.2	254	+10
Lake Tekapo	6.8	-0.1	2.9	+1.2	11.0	-5.0	51	-2
Tara Hills	7.2	-1.1	3.1	+1.8	10.8	-6.3	51	+11
August 1978								
The Hermitage	8.7	0.5	4.6	+1.0	17.5	-3.8	436	+154
Lake Tekapo	9.7	-0.3	4.7	+1.1	15.5	-3.0	101	+53
Tara Hills	10.4	-0.5	5.0	+1.3	15.4	-8.9	68	+38
September 1978								
The Hermitage	10.6	1.6	6.1	-0.3	18.0	-1.7	368	+138
Lake Tekapo	10.6	1.8	6.2	-0.8	16.2	-2.0	44	-12
Tara Hills	11.7	2.1	6.9	-0.1	16.4	-2.6	45	+9
October 1978								
The Hermitage	14.5	3.3	8.9	+0.1	22.3	-2.5	292	-79
Lake Tekapo	15.2	3.6	9.4	-0.2	23.0	-0.5	41	-10
Tara Hills	15.7	3.3	9.5	-0.3	22.5	-1.9	54	+6
November 1978								
The Hermitage	16.1	5.6	10.9	+0.5	26.1	-1.2	381	-18
Lake Tekapo	17.9	5.5	11.7	+0.2	27.2	0.0	32	-19
Tara Hills	18.9	5.9	12.4	+0.5	28.9	-0.8	49	+1
December 1978								
The Hermitage	17.8	7.3	12.6	+0.1	25.6	0.1	216	-170
Lake Tekapo	18.3	8.4	13.4	-0.3	25.5	2.5	13	+17
Tara Hills	20.6	8.4	14.5	+0.4	27.2	3.7	13	-10

APPENDIX A cont..

	Average Maximum	Average Minimum	Average	Deviation from Normal	Extreme Maximum	Extreme Minimum	Total mm	Deviation from Normal
January 1979								
The Hermitage	19.9	8.9	14.4	+0.3	26.5	2.0	326	-75
Lake Takapo	22.6	9.4	16.0	+0.7	27.9	2.0	8	-43
Tara Hills	24.3	7.8	16.1	+0.3	30.1	0.3	6	-58
February 1979								
The Hermitage	19.5	8.2	13.9	-0.1	29.5	4.6	465	+74
Lake Tekapo	21.1	8.6	14.9	-0.3	29.5	0.4	34	-9
Tara Hills	22.8	7.5	15.4	0.0	32.5	1.5	49	-7
March 1979								
The Hermitage	16.0	8.0	12.0	-0.3	23.0	-0.2	638	+285
Lake Tekapo	17.1	8.0	12.6	-0.5	22.5	-0.4	72	+24
Tara Hills	18.4	9.0	13.7	+0.5	24.9	1.8	110	+57
April 1979								
The Hermitage	13.4	3.7	8.6	-0.4	18.3	-2.0	408	+68
Lake Tekapo	14.1	3.9	9.0	-7.0	19.8	-1.4	40	-13
Tara Hills	14.6	4.1	9.4	0.0	19.5	-2.9	43	0

APPENDIX B

STATISTICAL PARAMETERS OF REGRESSIONS BETWEEN GROWTH INDICES AND PLANT DRY WEIGHTS

The relationships are given in the form:

$$y = a + bX + cX^2 + \text{etc.},$$

where Y = $\log_e$ (dry weight milligrams) and X = growth index, and where the numerical coefficients (a, b, c, etc.) were determined by regression analysis. Reliability parameters of these relationships are given within brackets. Numbers in the first bracket are:

(1) sample size,

(2) standard error of estimate of the equation, and

(3) square of multiple correlation efficient which gives the percentage variation of dependent variable accounted for by the fitted equation.

The numbers in the second bracket are, for each coefficient in the equation, the standard errors of that coefficient expressed as a percentage of the coefficient. The inverse of these are the "t" values for testing level of significance where appropriate.

Species	Plant part	Site	
H. pilosella	Leaves	Acherons	$Y = 0.606 + 0.828X - 0.0428X^2$ (90, 0.21, 96)(14, 5, 9)
"	"	Ruataniwha	$Y = 0.723 + 0.710X - 0.0340X^2$ (90, 0.18, 97)(10, 5, 9)
"	"	Wolds 1	$Y = 1.116 + 0.582X - 0.0200X^2$ (90, 0.22, 95)(8, 7, 20)

Appendix B (cont.)

Species	Plant part	Site	
H. pilosella	Leaves	Sawdon	$Y = 0.510 + 0.783X - 0.0394X^2$
			(100, 0.20, 97) (14, 4, 7)
"	"	Glentanner	$Y = 0.493 + 0.797X - 0.0414X^2$
			(110, 0.26, 94) (20, 4, 7)
"	Stolons	Acherons	$Y = 2.932 + 0.219X$
			(70, 0.34, 60) (3,10)
"	"	Ruataniwha	$Y = 2.768 + 0.207X$
			(63, 0.30, 71) (2, 8)
"	"	Wolds 1	$Y = 2.227 + 0.317X - 0.0132X^2 + 0.00021X^3$
			(70, 0.29, 93) (4, 12, 23, 31)
"	"	Sawdon	$Y = 2.639 + 0.208X$
			(60, 0.23, 67) (2, 9)
"	"	Glentanner	$Y = 2.267 + 0.834X - 0.195X^2 + 0.017X^3$
			(80, 0.26, 80) (6, 19, 25, 24)
H. praealtum	Leaves	Acherons	$Y = 0.856 + 0.955X - 0.0931X^2 + 0.00441X^2$
			(90, 0.26, 95) (20, 15, 35, 49)
"	"	Ruataniwha	$Y = 0.823 + 1.017X - 0.0843X^2 + 0.00264X^3$
			(100, 0.19, 97) (14, 8, 27, 40)
"	"	Wolds 1	$Y = 0.273 + 1.637X - 0.173X^2 + 0.00657X^3$
			(110, 0.24, 97) (49, 6, 10, 15)
"	"	Glentanner	$Y = 0.837 + 0.629X - 0.0214X^2$
			(110, 0.25, 96) (10, 5, 13)
"	Stolons	Acherons	$Y = 2.735 + 2.295X - 0.494X^2$
			(30, 0.20, 92) (8, 18, 33)

Appendix B (cont.)

Species	Plant part	Site	
H. praealtum	Stolons	Ruataniwha	$Y = 2.363 + 1.241X - 0.195X^2$
			(30, 0.21, 80)(12, 26, 41)
"	"	Wolds 1	$Y = 3.151 + 0.595X - 0.0318X^2$
			(50, 0.50, 64)(11, 22, 33)
"	"	Glentanner	$Y = 3.729 + 0.834X$
			(30, 0.28, 78)(3, 10)

Density of spring plants dm^{-2}

Species	Site				
	Acherons	Ruataniwha	Wolds	Sawdon	Glentanner
H. pilosella	23.40	21.48	25.36	30.25	32.80
H. praealtum	11.44	12.48	12.44		8.84

Parallel harvests of inflorescences and scapes at four stages (see Chapter 3 for details). Dates 1, 2 and 3 for primary daughter harvests were the last three sampling dates (see tables of indirect indices below).

Species	Site	Harvest weight ($\bar{Y}$±Se) in milligrams: n=10						
		Inflorescence and scape stage				Daughter at date		
H. pilosella		1	2	3	4	1	2	3
"	Acherons	13±2	37±5	59±12	82±12	21±7	43±10	59±14
"	Ruataniwha	16±4	37±4	43±7	81±18	14±3	48±12	59±13
"	Wolds 1	16±2	47±5	92±16	118±22	16±7	146±38	146±30
"	Sawdon	10±2	38±7	61±10	82±14	7±1	15±4	22±5
"	Glentanner	12±4	35±4	66±14	90±15	12±5	26±9	36±11
H. praealtum	Acherons	13±2	37±5	59±12	83±12	46±13	80±19	69±20
"	Ruataniwha	23±4	45±6	124±29	239±48	59±14	139±43	158±70
"	Wolds 1	29±6	47±16	92±32	381±55	142±87	212±42	379±65
"	Glentanner	15±5	28±5	67±15	162±19	47±14	78±12	116±44

GROWTH INDICES AND SAMPLING DATES PER 100 PLANTS

na = no further additions

ACHERONS SITE

H. pilosella

Date	Leaf number $\bar{Y}$±se	Stolon length $\bar{Y}$±se	Number of stolons	Inflorescence/scape stage number 1	2	3	4
1/9/78	0.65±0.58	0	0	0	0	0	0
12/9/78	1.17±0.74	0	0	0	0	0	0
26/9/78	3.04±1.09	0	0	0	0	0	0
11/10/78	4.57±1.22	0	0	0	0	0	0
26/10/78	5.43±1.43	0	0	8	0	0	0
16/11/78	6.75±1.52	S	S	26	0	0	0
28/11/78	7.42±1.56	2.23±1.47	11	26	1	10	0
21/12/78	8.12±1.55	3.89±2.97	22	11	12	7	21
21/1/79	8.45±1.62	1.93±2.78	64	6	0	2	45
12/2/79	8.62±1.69	1.92±2.70	68	na	na	na	na
13/3/79	8.93±1.93	na	na	na	na	na	na
19/4/79	9.58±2.40	na	na	na	na	na	an

H. praealtum

1/9/78	1.00±0.78	0	0	0	0	0	0
12/9/78	1.76±0.93	0	0	0	0	0	0
26/9/78	3.68±1.20	0	0	0	0	0	0
11/10/78	5.22±1.31	0	0	0	0	0	0
26/10/78	6.30±1.46	0	0	0	0	0	0
16/11/78	7.52±1.47	S	S	40	0	0	0
28/11/78	7.92±1.41	S	S	5	22	14	4
22/12/78	8.53±1.35	1.42±0.66	6	2	3	3	38
21/1/79	8.73±1.48	1.25±0.92	42	na	na	na	na
12/2/79	8.83±1.51	1.21±0.87	51	na	na	na	na
13/3/79	9.41±2.22	na	na	na	na	na	na
19/4/79	9.99±3.03	na	na	na	na	na	na

S = stolons

Appendix B (cont.)

RUATANIWHA SITE

H. pilosella

Date	Leaf number $\bar{Y}$±se	Stolon length $\bar{Y}$±se	Number of stolons	Inflorescence/scape stage 1	2	3	4
31/8/78	0.12±0.33	0	0	0	0	0	0
13/9/78	0.70±0.73	0	0	0	0	0	0
26/9/78	2.63±1.02	0	0	0	0	0	0
11/10/78	4.10±1.31	0	0	0	0	0	0
26/10/78	4.93±1.34	S	S	13	0	32	1
15/11/78	6.07±1.08	3.77±3.25	35	43	0	0	0
28/11/78	6.67±1.19	4.89±3.79	35	21	0	0	0
22/12/78	7.39±1.41	6.55±4.96	49	4	6	11	37
20/1/79	7.82±1.71	4.42±4.93	90	1	0	6	54
13/2/79	8.00±1.85	4.50±5.05	102	1	0	4	56
13/3/79	8.38±2.15	na	na	na	na	na	na
18/4/79	9.00±2.69	na	na	na	na	na	na

H. praealtum

31/8/78	0.75±0.69	0	0	0	0	0	0
13/9/78	2.83±1.06	0	0	0	0	0	0
26/9/78	5.18±1.25	0	0	0	0	0	0
11/10/78	6.97±1.52	0	0	0	0	0	0
26/10/78	8.41±1.76	0	0	0	0	0	0
15/11/78	9.33±1.68	S	S	48	20	0	0
28/11/78	9.71±1.57	S	S	na	7	70	
21/12/78	9.94±1.54	2.79±1.32	24	na	na	7	74
20/1/79	10.07±1.63	1.55±1.77	131	na	na	5	76
13/2/79	10.18±1.75	1.39±1.60	159	na	na	na	na
13/3/79	10.55±2.28	na	na	na	na	na	na
18/4/79	10.89±2.92	na	na	na	na	na	na

S = stolons

Appendix B (cont.)

WOLDS 1 SITE

H. pilosella

Date	Leaf number $\bar{Y}$±se	Stolon length $\bar{Y}$±se	Number of stolons	Inflorescence/scape stage 1	2	3	4
14/9/78	2.37±0.87	0	0	0	0	0	0
27/9/78	4.23±1.14	0	0	0	0	0	0
10/10/78	5.95±1.38	0	0	0	0	0	0
25/10/78	6.95±1.36	2.0±1.0	3	29	0	0	0
16/11/78	8.05±1.39	6.90±4.26	71	70	1	0	0
30/11/78	8.66±1.48	9.67±7.60	112	62	19	1	
18/12/78	9.05±1.54	11.61±7.63	147	33	13	14	22
17/1/79	9.38±1.85	12.21±7.29	168	28	13	18	23
9/2/79	9.45±1.91	12.45±7.58	173	26	13	18	26
12/3/79	9.57±2.09	na	na	na	na	na	na
17/4/79	9.88±2.57	na	na	na	na	na	na

H. praealtum

14/9/78	3.69±0.88	0	0	0	0	0	0
27/9/78	5.80±1.11	0	0	0	0	0	0
10/10/78	7.76±1.28	0	0	0	0	0	0
25/10/78	9.27±1.49	0	0	0	0	0	0
15/11/78	.65±1.54	S	S	85	0	0	0
30/11/78	10.87±1.57	S	S	22	23	42	1
18/12/78	10.95±1.58	1.77±3.49	124	16	18	15	43
18/1/79	11.06±1.69	4.83±3.20	233	14	19	16	43
9/2/79	11.11±1.81	4.75±3.45	291	14	20	16	45
12/3/79	11.25±2.01	na	na	na	na	na	na
17/4/79	11.35+2.26	na	na	na	na	na	na

S = stolons

Appendix B (cont.)

SAWDON SITE

H. pilosella

Date	Leaf number $\bar{Y}$±se	Stolon length $\bar{Y}$±se	Number of stolons	Inflorescence/scape stage			
				1	2	3	4
14/9/78	0.55±0.67	0	0	0	0	0	0
29/9/78	2.01±0.85	0	0	0	0	0	0
10/10/78	3.17±0.02	0	0	0	0	0	0
24/10/78	4.00±1.02	0	0	0	0	0	0
14/11/78	5.25±13.1	0	0	0	0	0	0
30/11/78	6.00±1.28	2.00	1	1	0	0	0
19/12/78	6.91±1.37	3.00	1	2	0	1	0
8/1/79	7.66±1.49	4.00	1	0	0	2	1
26/1/79	8.01±1.54	1.83	3	0	0	1	2
8/2/79	8.18±1.56	1.62	4	0	0	1	2
14/3/79	8.30±1.62	1.63	4	0	0	1	2
18/4/79	8.55±1.72	1.50	5	0	0	1	2

GLENTANNER SITE

H. pilosella

Date	Leaf number $\bar{Y}$±se	Stolon length $\bar{Y}$±se	Number of stolons	Inflorescence/scape stage 1	2	3	4
28/9/78	1.72±0.60	0	0	0	0	0	0
12/10/78	3.28±0.82	0	0	0	0	0	0
25/10/78	4.18±0.95	0	0	0	0	0	0
17/11/78	5.84±1.20	S	S	13	0	0	0
29/11/78	6.63±1.23	1.20±0.45	5	22	0	0	0
20/12/78	7.30±1.17	3.77±2.11	9	10	16	8	0
9/1/79	7.98±1.24	3.71±2.78	16	0	3	8	23
10/2/79	8.71±1.45	1.56±2.05	53	0	0	0	34
13/3/79	9.22±1.76	na	na	0	0	0	na
18/4/79	9.67±2.15	na	na	0	0	0	na

H. praealtum

28/9/78	4.13±0.85			0	0	0	0
12/10/78	5.85±0.98			0	0	0	0
25/10/78	7.15±1.03			0	0	0	0
17/11/78	8.89±1.29	S	S	92	0	0	0
29/11/78	9.00±1.14	S	S	2	70	21	0
20/12/78	9.10±1.07	2.65±0.93	17	3	4	12	74
9/1/79	9.21±1.09	1.90±1.11	73	2	2	0	89
10/2/79	9.38±1.31	1.19±0.89	167	na	na	na	na
13/3/79	9.57±1.77	na	na	na	na	na	na
18/4/79	9.77±2.24	na	na	na	na	na	na

S = stolons